EXPERIMENTAL STUDIES ON THE NATURE OF SPECIES

IV. GENETIC STRUCTURE OF ECOLOGICAL RACES

JENS CLAUSEN
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CARNEGIE INSTITUTION OF WASHINGTON PUBLICATION 615

WASHINGTON, D. C.

1958

Library of Congress Catalog Card Number 50–14859

THE LORD BALTIMORE PRESS, INC., BALTIMORE, MARYLAND

PREFACE

Ecological genetics is a new integrating field in biology for which the principles have not been formally stated. Its objective is study of the hereditary structure that controls the mechanisms and processes through which ecological races and species have become adjusted to their environments.

It is of basic importance to understand the hereditary mechanisms that function in the perpetuation of the existing natural races and species and in the evolution of new ones, but investigations in this field are difficult and have largely been neglected. The commonly used laboratory organisms are inadequate to resolve differences that characterize natural biological entities found in the wild.

Three areas of investigation contribute to ecological genetics. One is a Mendelian analysis of the genes that control the inheritance of the individual characters of ecological races. Another, and almost untouched, field is the study of the expression of the genes in different kinds of environment. The third field, whose development also lies in the future, is the mapping of the pathways or mechanisms through which the genes act to produce their observed end effects in diverse environments. All three areas of study are closely interrelated. They bear directly on the dynamics of natural populations, and on the evolution of species in the wild.

The ecological races of *Potentilla glandulosa* are particularly well suited for such investigations. The species is widespread over the western half of the North American continent, and close relatives encircle the Northern Hemisphere. All the races of *Potentilla glandulosa* are diploid with seven pairs of chromosomes, and even the most contrasting forms of the species are intercrossable and interfertile.

The numerous races of *Potentilla glandulosa* inhabit a wide range of climates, from the subtropical winter rain belts to frigid alpine regions of the high mountains. They differ so much in morphology that several have been described as distinct species; accordingly, they have characters suitable to serve as morphological markers in genetic experiments.

Potentilla glandulosa is a long-lived perennial which can be readily cloned and observed over a period of years after transplantation to contrasting climates. Its longevity is combined with slow development, so that long periods of time are required for the completion of such experiments; but this character also offers opportunity to study annual fluctuations in the expression of characters. The original crossings in our research project were made in 1932. The process of growing and studying the progeny in contrasting environments has been carried on ever since.

The present volume comprises: (1) an inquiry into the population structure of ecological races and subspecies of *Potentilla glandulosa* along an altitudinal transect at approximately 38° north latitude in central California; (2) an analy-

sis of the genetic structure of selected individuals of the races through their F_2 and F_3 progeny; (3) a report on the responses of cloned individuals of an interracial F_2 population in the environments of three contrasting altitudinal transplant stations; (4) an integration of the findings of the present experiments with those recorded in many organisms through the first fifty years of modern genetics; and (5) a presentation of the authors' conclusions based on the available evidence.

Acknowledgments

The authors acknowledge with gratitude their indebtedness to their former colleague and collaborator, Dr. David D. Keck, now Assistant Director of the New York Botanical Garden, who took an active part in the planning of the experimental work described in this volume, in the recording of data, and in the early stages of the preparation of the manuscript, including some of the illustrations. Dr. Helen K. Sharsmith, now at the Department of Botany, University of California, Berkeley, made valuable contributions in the computation of statistical data used in this volume, and Dr. Lincoln E. Moses, Associate Professor of Statistics, Stanford University, gave freely of his time for consultations. Mrs. Marion S. Bracken, Mrs. Alberta S. Caswell, and Mrs. Sigrid Sierra at different stages of the work on the manuscript have devoted painstaking effort to preparing the typescript. As in earlier monographs of this series, the photographic skill of Mr. Berton Crandall, of Palo Alto, is evident in many of the illustrations. Many of the line drawings presented in chapters I to III were made by Mr. Stanley Dunphy, an advanced art student at Stanford University.

To colleagues too numerous to name individually, representing different fields and points of view at scientific institutions in countries on five continents, the authors owe a special debt of gratitude for helpful criticism and discussion of topics pertinent to the subject matter at hand.

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September 15, 1956

CONTENTS

CHAPTER PAGE

I. THE ECOLOGICAL RACES OF POTENTILLA GLANDULOSA . . . 1

Region of origin of experimental plants, 1. Natural composition of the species, 2. Subspecies in *Potentilla glandulosa,* 2. Subspecies *typica,* 5. Subspecies *reflexa,* 14. Subspecies *hanseni,* 18. Subspecies *nevadensis,* 21. Intergrades between subspecies, 24. Conclusions concerning the composition of *Potentilla glandulosa,* 25.

II. GENETICS OF ECOLOGICAL RACES 29

MATERIALS AND METHODS 29

The races crossed, 29. General methods, 29. Use of punched cards in analysis of data, 32.

THE SEGREGATING HYBRID PROGENIES 35

Upper Monarch Lake × Santa Barbara, 35. Index values of F_2's of the cross Upper Monarch Lake × Santa Barbara, 38. Segregation of akene weight in Upper Monarch Lake × Santa Barbara, 39. Timberline × Oak Grove, 45. Index values in the cross Timberline × Oak Grove, 49. F_3 populations of the cross Timberline × Oak Grove, 49.

GENIC ANALYSIS OF CHARACTERS 54

1, Orientation of petals, 54. 2, Petal notch, 57. 3, Petal color, 61. 4, Petal width, 65. 5, Petal length, 71. 6, Sepal length, 74. 7, Akene weight, 76. 8, Akene color, 76. 9, Branching of the inflorescence, 77. 10, Density of inflorescence, 78. 11, Crown height, 79. 12, Anthocyanin, 80. 13, Pubescence, 88. 14, Length of leaves, 89. 15, Number of leaflets on leaves subtending the inflorescence, 93. 16, Stem length, 94. 17, Winter dormancy, 101. 18, Frost susceptibility, 103. 19, Earliness of flowering, 105. Minimum number of genes regulating differences between races of *Potentilla,* 108.

GENETIC CORRELATION 110

Method used in determining genetic correlation, 111. Results of correlation studies, 112. Upper Monarch Lake × Santa Barbara, 114. Timberline × Oak Grove, 116. Effects of certain genetic systems on correlation between characters, 117.

III. RESPONSE PATTERNS AT CONTRASTING ALTITUDES 123

MODIFICATIONS OF CHARACTERS 127

1, Leaf length, 130. 2, Rosette width, 136. 3, Stem length, 137. 4, Stem number, 138. 5, Vigor, 138. 6, Date of first flowers, 139. 7, Survival, 139. 8, Patterns of survival, 140.

GENETIC RECOMBINATION AND CORRELATION IN PATTERNS OF RESPONSE 141

1, Fractions sorted on the basis of vigor in three environments, 142. 2, Fractions sorted on the basis of stem length, 146. 3, Fractions separated on the basis of earliness of flowering, 147.

SHIFTS IN CORRELATION FROM STATION TO STATION 150

CHAPTER PAGE

Correlation between Survival Capacity and Parental Characteristics ... 151

Selection of Specified Fractions of F_2 Progeny ... 153

Conclusions ... 155

IV. SYSTEMS OF GENES CONTROLLING CHARACTERS AND THEIR SIGNIFICANCE IN ENVIRONMENTAL ADAPTATION AND EVOLUTION ... 157

Genetic Systems Regulating Individual Characters ... 160

Complementary genes in *Lathyrus odoratus* L., 160. Complementary and inhibitory genes governing color of plumage in poultry, 161. Polymeric genes in wheats and oats and transgressive segregation, 161. Transgressive segregation in *Nicotiana,* 165. Gene systems regulating quantitative characters in maize, 167. Oppositional genes governing aleurone color, 168. Plant colors in maize, 169. Genes inhibiting the development of stripes in the shell of snails, 171. Shape of leaves and capsules in *Capsella,* 171. Inheritance of leaf shape and stellate pubescence in *Camelina,* 176. Multiple genes in diploid *Crepis,* 176. Multiple genes governing seed size in peas, 179. Genes controlling pod shape in peas, 181. Genes of oppositional effect controlling fruit shape in *Cucurbita,* 184. Multiple genes in *Lamium,* 184. *Plantago major,* 185. Multiple genes in *Drosophila melanogaster,* 187. Systems of genes in wild pansies, *Viola tricolor* and *V. arvensis,* 187. Gene systems in *Layia,* 190. A system of oppositional genes governing time of flowering in *Madia,* 192.

Gene Systems Regulating Biochemical and Physiological Effects and Their Expression in Different Environments ... 193

The physiological action of waxy versus starchy gene in maize, 194. Multiple genes in yeasts controlling the production of enzymes, 195. Complementary genes governing cyanogenesis in legumes, 199. Phenotypic expression of genotypes over a range of environments, 200. Variation expressed beyond the natural environmental range of the organism, 202.

Genetic Systems of Ecological Races of Plants ... 203

Inheritance in maritime and inland races of plants, *Silene,* 203. Genetic control of maritime and inland races of *Viola tricolor,* 204. Genetic mechanisms distinguishing maritime and inland ecotypes of the Madiinae, 205. Coast Range and Central Valley ecotypes in a weedy bromegrass, 206. Genetic control of ecological races in *Geranium robertianum,* 207. Ecotypic subspecies in *Gilia capitata,* 207. Ecotypes and ecotypic subspecies in *Solidago,* 209. Ecotypes and geographic subspecies of the *Plantago maritima* complex, 210. Ecotypic subspecies within the *Armeria maritima* complex, 212. Altitudinal races in the *Mimulus guttatus* complex, 214. Genetic and physiological characteristics of species and altitudinal races of the *Achillea millefolium* complex, 217. Seasonal ecotypes within *Lamium purpureum,* 219. Inherit-

CHAPTER PAGE

ance of the annual and biennial character in *Melilotus,* 220. Seasonal and climatic races in the Madiinae, 222. Genetic-physiologic control of periodicity in *Lolium,* 224. Genetic-physiologic control of flowering in *Sorghum,* 228. Ecological differentiation within apomictic Poas, 232.

Genetic Systems Differentiating Subspecies and Other Taxonomic Entities in Plants 235

Inheritance in the *Geum urbanum-rivale* complex, 235. Subspecific differences in *Layia* involving characters of tribal significance, 243. Inheritance in spatially isolated subspecies of *Hemizonia angustifolia,* 245. Intercontinental subspecific differentiation in *Platanus,* 246.

Genetics of Ecological Races in the Animal Kingdom 247

Altitudinal and seasonal variation in *Drosophila,* 247. Genetic-physiologic incompatibility between regional ecologic races of *Rana pipiens,* 251. Heredity of adaptive characters in ecologic races of *Lymantria,* 255.

V. CONCEPTS OF THE GENETIC STRUCTURE OF ECOLOGICAL RACES 263

Systems of genes controlling individual characters, 263. Ranges of environment within which genes may be expressed, 264. The unanalyzed part of the genotype, 265. Release of variability, 265. Coherence of characters distinguishing ecological races, 266. Interaction among genes, processes, and environment, 266. Hybrid vigor, 268. Ecological races as reservoirs of genes, 268.

LITERATURE CITED 270

INDEX 283

I

THE ECOLOGICAL RACES OF POTENTILLA GLANDULOSA

The first step in an analysis of ecological races is the study in a uniform environment of the components of widespread species that occupy a great diversity of environments, and the mapping of their distribution. Volume I of this series (Clausen, Keck, and Hiesey, 1940) presented a great deal of evidence on what was then known of the ecological races of *Potentilla glandulosa* Lindl., of its allies, and of many other species of western North American plants. Volume III of the same series (Clausen, Keck, and Hiesey, 1948) was devoted to a comprehensive analysis of the very diverse climatic races of the *Achillea millefolium* complex found along a transect across central California.

This first chapter will present data on a more thorough analysis of the ecological races of *Potentilla glandulosa* along the same transect. The new evidence will be integrated with that previously given, and will provide a background both for the genetic analysis discussed in chapter II and for the selection studies in different environments described in chapter III.

Since our aim is to clarify general principles of relationships among higher plants, we shall also compare the races of *Potentilla glandulosa* with those of other groups along the same transect whose races have been studied in detail, especially with *Achillea*. The seeds for many of the population samples of *Achillea* and *Potentilla* were taken at the same localities along the Sierran transect, so that direct comparison is possible between comparable samples of the two genera, the former belonging to the family Compositae, and the latter to the Rosaceae.

Region of origin of experimental plants. The current studies largely center along the transect in central California from the Pacific Ocean eastward to the Great Basin region in the vicinity of 38° north latitude. The wide differences in topography, altitude, and climate across this region were described in Volumes I and III of this series.

The experiment gardens maintained by the Carnegie Institution of Washington at three contrasting altitudes are also described in these publications. The three stations are located at Stanford, between the outer and inner Coast Ranges at 30 m. altitude; at Mather, on the western slope of the Sierra Nevada, at 1400 m.; and at Timberline, at 3050 m., north of Tioga Pass and east of the crest of the Sierra Nevada. Stanford has the mildest climate, Timberline the most severe, and Mather is intermediate. A series of temperature and precipitation graphs in Volume III (Clausen, Keck, and Hiesey, 1948; see pp. 8–16) depict the climatic variation along the transect from which the samples of *Potentilla* and *Achillea* were taken.

The climate along this 200-mile transect presents great diversity, ranging from the mild, year-round growing conditions of the coast to the long winters and very short summers of alpine areas. Many species are restricted in distribution

to small sectors, and as a consequence many kinds of plant communities can be found along the transect. The western slope of the Sierra Nevada, extending from 100 to 3300 m. in altitude, is gradual, and affords a climatic gradient along which zones differing from one another in fairly regular sequence can be distinguished.

NATURAL COMPOSITION OF THE SPECIES. The forms of *Potentilla glandulosa* and its close relatives comprise a series of races fitted to survive in different climates, as was shown by the extensive transplant experiments described in the first volume of this series. Their fitness clearly rests on a physiological basis, which, in turn, is controlled by heredity.

The descriptive taxonomy, geographic distribution, and general relationships of *Potentilla glandulosa* and its allies were discussed in Volume I and will not be elaborated here. In the following pages both old and new evidence bearing on the composition of this species in relation to environment will be reviewed in some detail. It should be emphasized, however, that the sampling of the races even now is far too incomplete for an adequate understanding of the biological complexity of this group. Our present interpretation, therefore, can at best only approximate the true situation as it exists in the wild.

A series of Stanford-grown races and forms of *Potentilla glandulosa* from along the transect of central California is depicted in figure 1. These samples, grown from seed, represent populations and races from environments differing in altitude at intervals of approximately 300 m., as indicated on the profile of the central California transect. Since all the plants shown were grown in the same garden, the differences visible in figure 1 are obviously due to heredity. Only a few of the more conspicuous character differences, however, are evident in the illustration. The physiological differences of selective value, as well as many morphological differences, do not show in the photographed herbarium specimens. The interrelation between the physiological qualities of the plant and its morphological characters becomes much more evident when cloned individuals of the various races are grown simultaneously in several contrasting environments.

SUBSPECIES IN POTENTILLA GLANDULOSA. Four morphologically distinct subspecies having ecologically distinct ranges can be recognized along the central California transect, namely, *typica, reflexa* (Greene) Keck, *hanseni* (Greene) Keck, and *nevadensis* (S. Wats.) Keck. Representatives of several populations of each of these subspecies are illustrated in figure 1. Stanford-grown plants representing three populations of each subspecies are also shown in figure 2, which depicts differences found within the same subspecies at different altitudes.

Subspecies *typica* occurs chiefly in the Coast Ranges, but it is of such complex composition that it is not yet fully understood. Subspecies *reflexa* is found mostly on the warm foothills of the lower Sierra Nevada, but extends up to middle altitudes on the warmer and drier slopes. In range of distribution, sub-

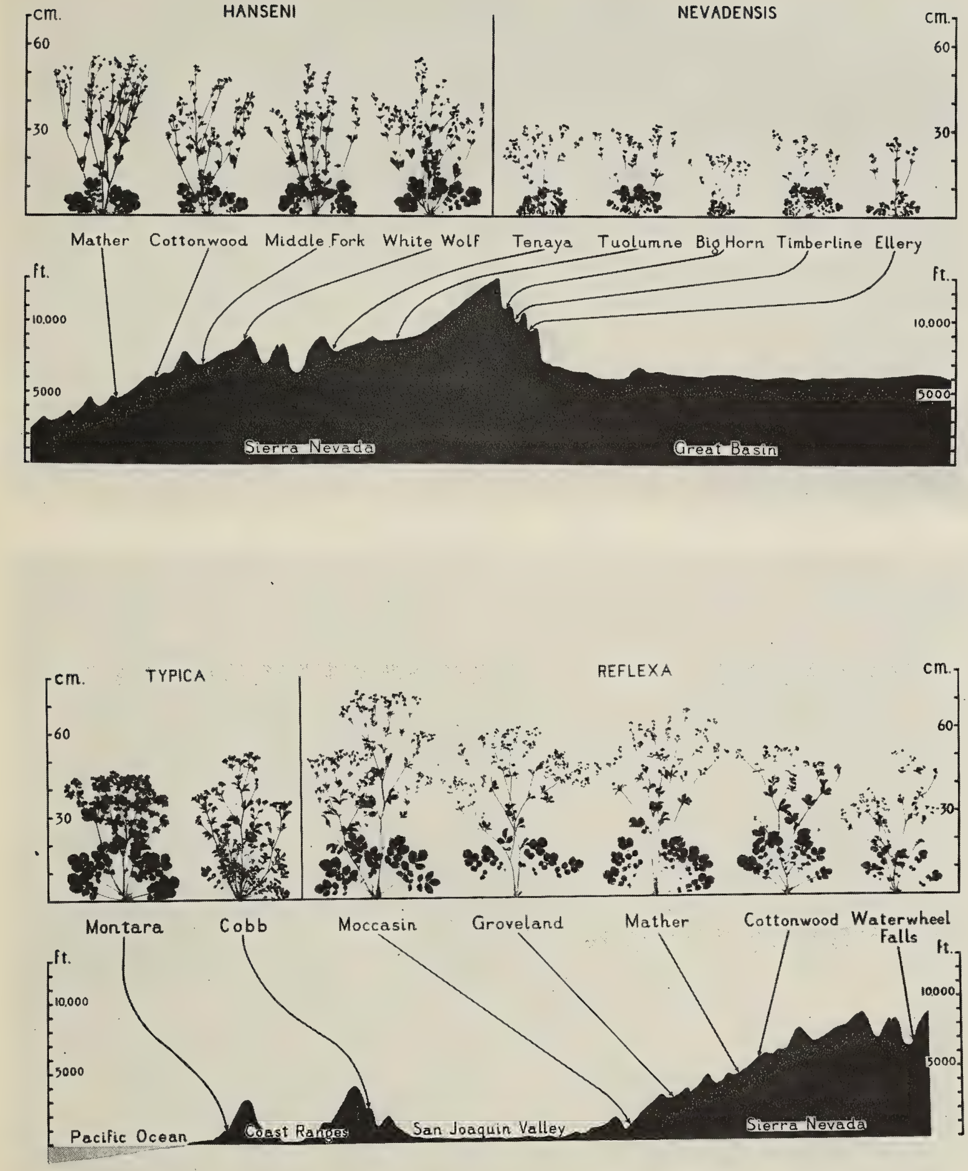

Fig. 1. Sample plants of populations of *Potentilla glandulosa* grown in a uniform garden at Stanford. The populations originated from the localities shown on the profile of a transect across central California at approximately 38° north latitude.

Below: the western half of the transect, starting at the Pacific coast. *Above:* the eastern half, extending to the Great Basin plateau; the two parts together represent an airline distance of approximately 200 miles. Altitudes are to scale in feet. Horizontal distances are not to scale.

The natural locations of the populations of the four subspecies *typica, reflexa, hanseni,* and *nevadensis* are indicated by the long arrows; *reflexa* and *hanseni* overlap in part of their ranges, as is seen in the partial duplication of the profile. The plants are herbarium specimens.

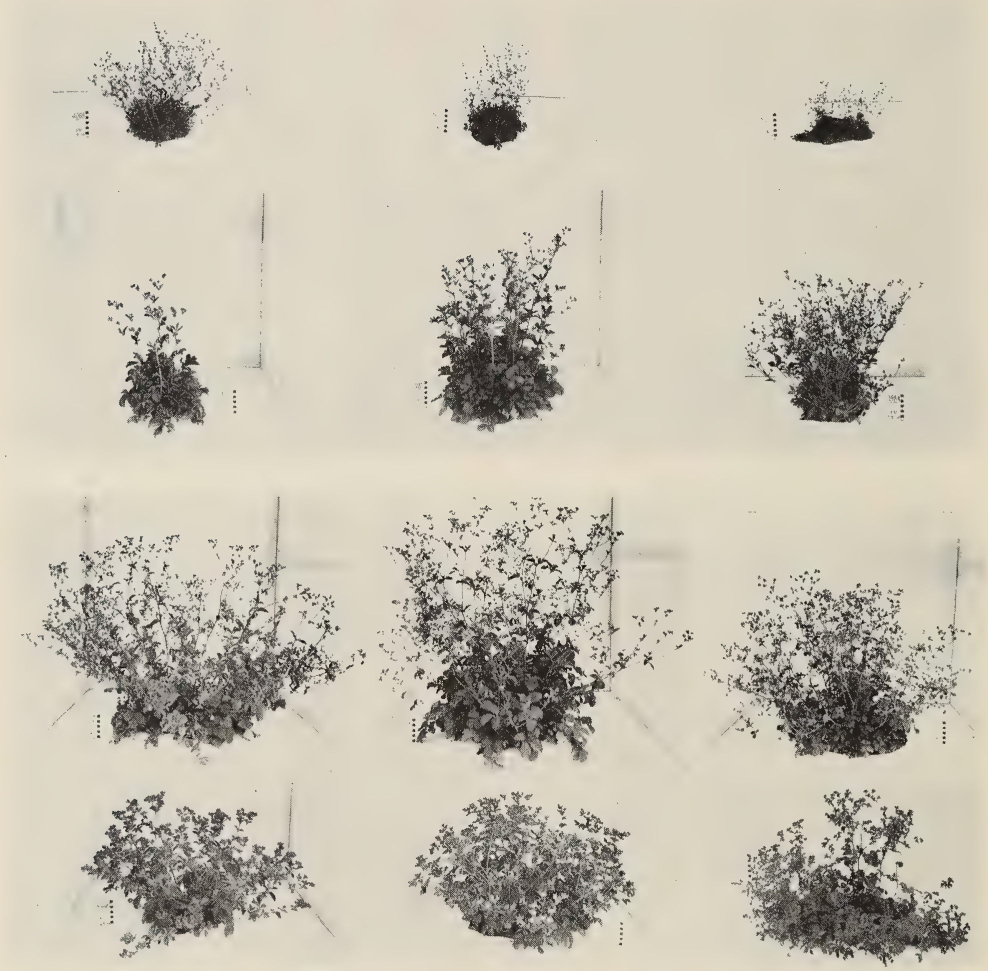

Fig. 2. Representatives of four subspecies of *Potentilla glandulosa* in a uniform garden at Stanford.

Lowermost row, typica: left, from Montara base at 60 m. altitude; *center,* Montara summit at 275 m.; and *right,* Santa Cruz Mts. at 560 m., all in San Mateo County, California.

Second row, reflexa: left, from Moccasin at 250 m.; *center,* Hetch Hetchy at 1190 m.; and *right,* Cottonwood at 1650 m., all in Tuolumne County, California.

Third row, hanseni: left, from Mather at 1400 m.; *center,* Smith Meadow at 1950 m.; and *right,* White Wolf at 2530 m., all in Tuolumne County, California.

Uppermost row, nevadensis: left, from Tenaya Lake at 2590 m., Tuolumne County; *center,* Timberline at 3170 m.; and *right,* Big Horn Lake at 3350 m., the latter two in Mono County, California.

The photographs were taken during the early summer of 1944; all are reproduced to the same scale.

species *hanseni* overlaps with *reflexa* and occurs at middle and higher altitudes in the Sierra Nevada. These two subspecies occupy edaphically distinct habitats; *hanseni* grows almost exclusively in moist meadowy habitats in intense competition with grasses and other herbaceous native plants, whereas *reflexa* occupies the drier slopes. The subspecies *nevadensis* is confined to the higher altitudes and grows mostly on sunny, well drained slopes, but always where there is a good supply of moisture during the active summer growing season. Table 1 lists the chief differences among these four subspecies.

On the basis of herbarium studies, other subspecies of *Potentilla glandulosa* were recognized and described in Volume I of this series: *glabrata* (Rydb.) Keck and *pseudorupestris* (Rydb.) Keck of the ranges in the northern part of the Great Basin, *micropetala* (Rydb.) Keck locally in Wyoming to Utah, and *arizonica* (Rydb.) Keck farther south from Utah to Arizona. Subspecies *glabrata* occurs at middle, and the others at high, altitudes. Three local subspecies were recognized farther west, namely, *ashlandica* (Greene) Keck of the Cascades and Siskiyous of southern Oregon, *globosa* Keck of the Siskiyous of southern Oregon and northern California, and *ewanii* Keck of the San Gabriel Mountains of southern California. Little is known of the ecology and physiological characteristics of these subspecies. Their distinctness was inferred only through such morphological characteristics as are observable in herbarium specimens, and their true composition and relation to one another and to their environment cannot be determined until they have been investigated experimentally. Closer study in the field would undoubtedly reveal the existence of additional morphologically recognizable entities. In the following pages the description will be confined largely to the subspecies *typica, reflexa, hanseni,* and *nevadensis,* which the writers have studied.

SUBSPECIES TYPICA. The subspecies to which the type specimen belongs is a form occurring essentially in the Coast Ranges of California. Forms that morphologically have been referred to that unit, however, have been listed northward to British Columbia and to eastern Idaho. The California Coast Range form of subspecies *typica* has relatively thick, coarse-veined leaves and large leafy bracts in the receptacle; densely villous and very glandular pubescence on the leaves and stems; green to purple divaricately branched stems; large sepals that much exceed the small, whitish to creamy-white petals; large, conical, and somewhat succulent receptacles; and large, dark brown akenes. The forms from the Coast Ranges are both winter- and summer-active when grown at Stanford, and they commence the season's growth in October to November when the winter rain period starts in its natural habitats.

In the warm-temperate gardens at Stanford between the outer and inner Coast Ranges *typica* grows with full vigor. It can survive in the more severe climate at Mather at 1400 m. altitude, where it is subjected to five months of cold winter. There it becomes winter-dormant and develops with reduced vigor, but during the summer it grows sufficiently to accumulate enough food

TABLE 1

SUMMARY OF PRINCIPAL DIFFERENCES AMONG FOUR SUBSPECIES OF POTENTILLA GLANDULOSA ALONG THE SIERRAN TRANSECT

Subspecies	*typica*	*reflexa*	*hanseni*	*nevadensis*
Distribution	Coast Ranges and lower Sierra Nevada	Slopes, low and middle altitudes of Sierra Nevada	Meadows, middle altitudes of Sierra Nevada	High altitudes of Sierra Nevada
Kinds of habitat	Soft chaparral and open woods	Dryish, openly timbered slopes	Moist meadows	Moist, sunny slopes
Climatic tolerance*	Coastal to middle altitudes	Middle altitudes to coast	Middle and high altitudes (poor survival near coast)	High and middle altitudes (poor survival near coast)
Seasonal periodicity at Stanford	Winter- and summer-active	Winter-active or -dormant, depending on ecotype; summer-active	Winter-dormant, summer-active	Winter-dormant, summer-active
Extent of variation within subspecies	Wide, probably several ecotypes	Wide, probably several ecotypes	Wide, at least two ecotypes	Moderate, at least two ecotypes
Self-compatibility	Self-fertile	Self-fertile	Undetermined	Self-sterile
Petals	Small, ascending-erect, cream-white	Small, reflexed, deep yellow	Medium, ascending, cream	Large, ascending, cream-white
Seeds	Large, dark brown	Medium, reddish brown	Medium, pale brown	Small, pale brown
Inflorescences	Divaricate, compact	Long-divaricate, open	Erect, ± open	Erect, fairly compact
Bracts of inflorescence	Large, leafy	Small	Medium	Very small
Leaves	Thick-textured, large	Thin-textured, large and long	Thick-textured, large	Thin-textured, small
Stems	Moderately tall, stout, spreading	Tall, slender, spreading	Tall (but highly modifiable), stout, erect	Short, very slender, erect
Pubescence	Dense, pilose	Fairly dense, pilose	Moderate, soft-pilose	Sparse
Glands	Abundant	Many	Few	Very few
Anthocyanin	Deeply to moderately anthocyanous to green	Deeply anthocyanous to green	Slightly to nonanthocyanous	Mostly nonanthocyanous
Crown	Fairly long, woody	Fairly long, woody	Short, ± woody	At ground level
Rhizomes	Few or none	Few or none	Few, fairly long	Many and long

* As determined by testing clones at the Stanford, Mather, and Timberline transplant stations.

reserves to carry it through the winter. Transplants of Coast Range *typica* brought to the much more severe climate at the Timberline station at 3000 m. altitude almost invariably die during the first winter.

These responses of *Potentilla glandulosa typica* to transplanting are parallel to those of coastal races of *Achillea borealis* Bong. described in Volume III of this series. The Coast Range races of both species are most vigorous in the lowland station at Stanford, because there they are able to grow during the rainy winter period as in their native habitats. At Mather both become dormant during the winter, but the fact that both are able to build up sufficient reserves during the summer to carry them through the fairly long winter demonstrates that races of both *Potentilla* and *Achillea* from outer Coast Ranges have a considerable range of tolerance to changes in climate. Neither is able to survive in the alpine climate at Timberline, however, even under the most favorable garden conditions.

Physiologically, the Coast Range races of *Potentilla glandulosa* and of *Achillea borealis* are therefore much more alike than the various climatic races within either species. That Coast Range races of other species have a similar pattern of reaction to transplanting to the three stations was pointed out in Volume I. The physiological qualities that characterize the coastal race of *Potentilla glandulosa typica* set it off as a biologically distinct unit having qualities in common with species of other genera and families that occur in that territory. Phylogenetically, however, it is closely allied to the other races of its own species.

Subspecies *typica* is nevertheless far from being homogeneous. Any one of its local populations from natural habitats shows individual variation, as is illustrated in figures 3 and 4 by the variation in size and shape of rosette leaves of distinct populations of the four subspecies of *Potentilla glandulosa* grown in a uniform garden at Stanford. The individual variation includes also small differences in habit, length of stems, pubescence, petal size, petal shape, and other characters, as is shown in table 3, page 16. Such morphological variations are hereditary, and represent minor biotypic differences between individuals of one population. Compared with the larger differences between the subspecies, the intrapopulation variations are of much less ecologic significance, although in the long-range evolution within the species they may play an important role.

Interpopulation differences within the same ecotype represent another step in intrasubspecific variation. An example is furnished by two populations of *typica,* both originating from Montara Mountain south of San Francisco and grown in a uniform garden at Stanford. One seed sample was collected from a large number of individuals in a protected canyon at 60 m. altitude near the base of the mountain a few miles from the sea. Another sample was taken from a more exposed colony at the top of the mountain at 275 m. altitude in a brush-covered locality overlooking the Pacific Ocean. The seeds from each colony were thoroughly mixed among themselves, and a sample of 60 individuals from each was grown in the Stanford garden. Each population was variable, and the two resembled each other closely except that the plants from the ex-

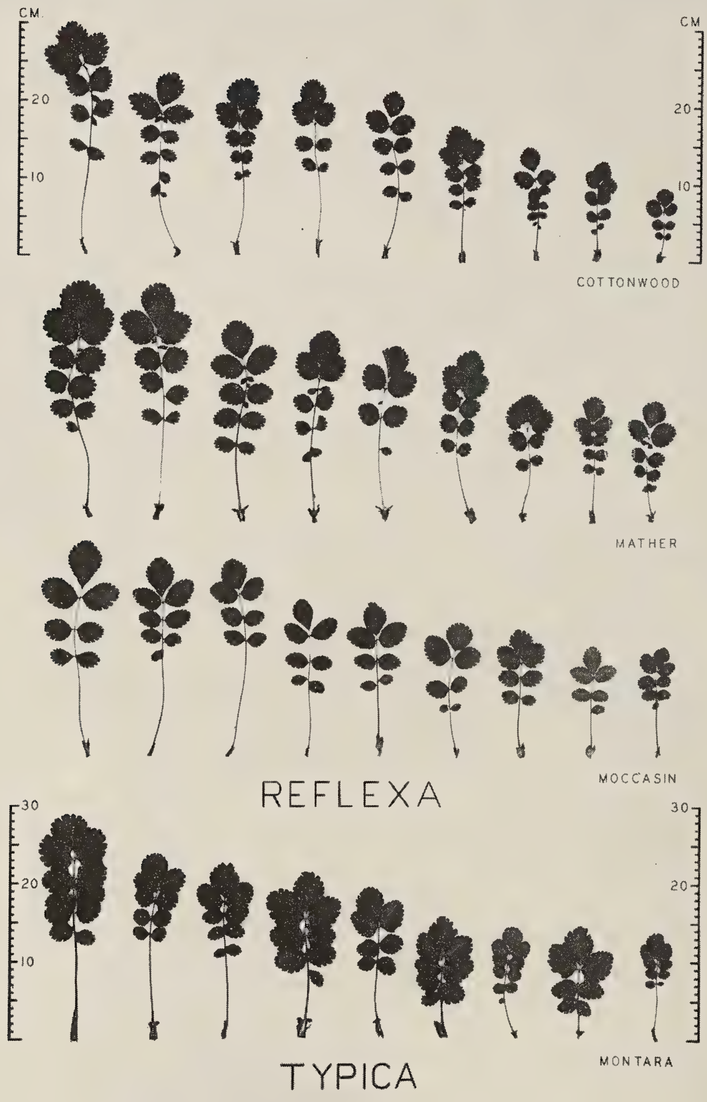

FIG. 3. Variation in rosette leaves among individuals of four populations grown in a uniform garden at Stanford.

Each leaf is from a different individual, and represents the longest typical leaves of the plant. The lowermost row shows leaves of subspecies *typica* from Montara; the upper rows, populations of subspecies *reflexa* from the locations indicated. See table 2 for further data on these populations.

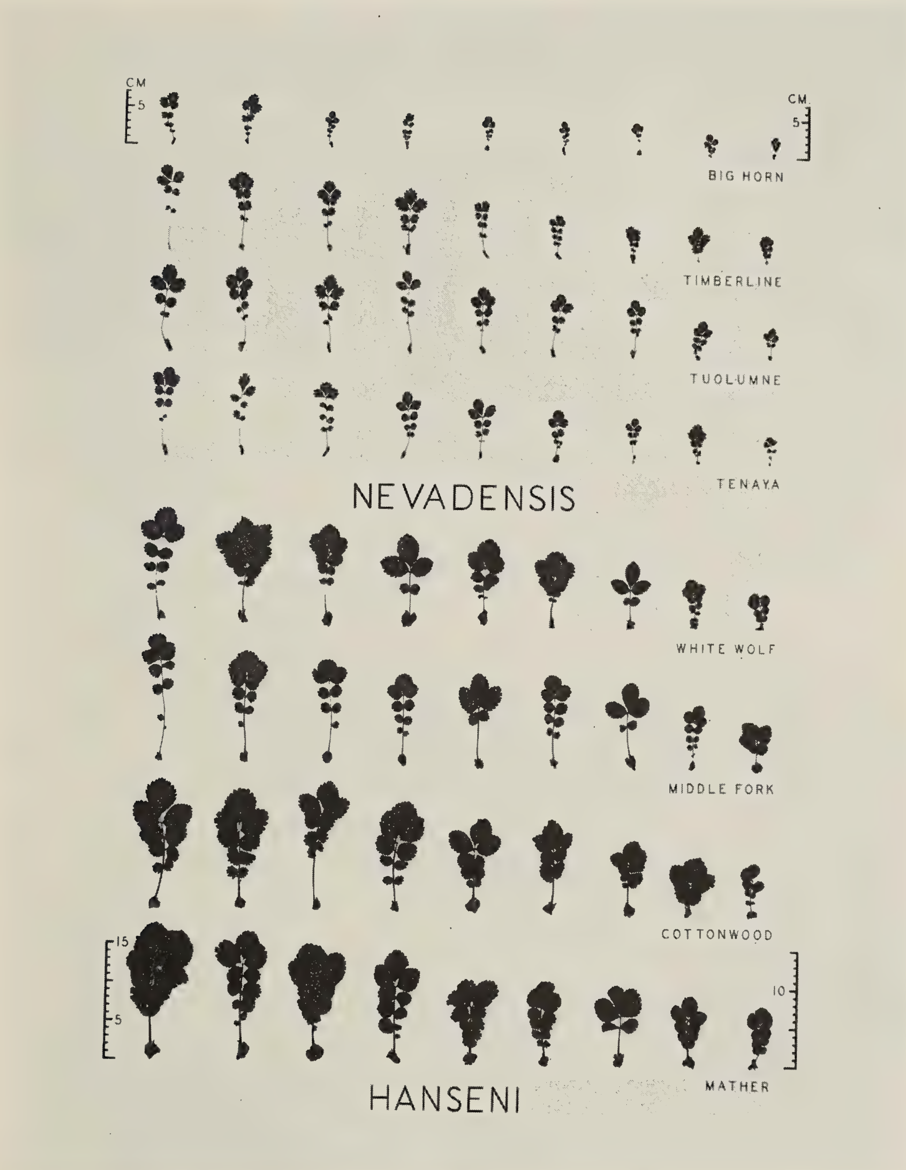

FIG. 4. Continuation from figure 3. The lowermost four rows are from populations of subspecies *hanseni* from the localities indicated, and the upper four rows are of subspecies *nevadensis*. See table 2 for further data regarding these populations.

posed summit of the mountain were significantly shorter-stemmed than those from the protected canyon. The individual variation within each population greatly overlapped that of the other.

The mean stem heights in centimeters for the two Montara populations 4060 and 4061 are given in table 2, which also lists leaf measurements, time and degree of flowering, and degree of winter activity at Stanford for these and 24 other populations of the four subspecies of *Potentilla glandulosa.* It is possible that natural selection was responsible for the genetically shorter and more divaricate characteristics of population 4061, collected in 1941 from the exposed Montara summit, in comparison with population 4060 from near the base.

At the summit location, 19 years earlier (1922), Dr. H. M. Hall collected living plants of this species a few years after the area had been swept by an extensive brush fire. Included in Hall's collection were very dwarf individuals having short stems half hidden in the leaf rosettes, as illustrated in Volume I of this series (Clausen, Keck, and Hiesey, 1940, fig. 14). Careful search for such dwarfs in 1941 failed, but meanwhile the extensive protective brush cover had reappeared, changing the biotic environment. Apparently the dwarf biotypes present in 1922 were favored by the absence of chaparral, whereas the reestablishment of shrubby vegetation in later years favored a shift in the composition of the population of *Potentilla glandulosa* toward taller forms.

A point of interest in connection with subspecies *typica* is that in the garden it will cross spontaneously with other subspecies of *glandulosa,* although it is highly self-fertile. One of the taller individuals collected by Hall from Montara summit (plant 1077-4, also illustrated in the figure cited above) was cloned and grown as a transplant at the three transplant stations. Seeds of the open-pollinated ramet of 1077-4 in the Mather garden were collected 17 years after the plant had been transplanted to the mid-altitude station. Sixty seedling progeny of this plant of coastal *typica* were raised to maturity at Stanford, and 4 proved to be F_1 hybrids with subspecies *hanseni,* native plants of which are common in the Mather garden. The remaining 56 plants were obviously selfed progeny having characteristics of regular *typica;* they are listed in table 2 under culture 3973.

It seems apparent, therefore, that populations of *typica* separated by only short distances of space and by relatively short periods of time at the same place may differ significantly in genetic composition. This subspecies has also the capacity for occasional outcrossing with other subspecies, even though *typica* is highly self-fertile and largely self-pollinated. The distinct populations of subspecies *typica* from the same general climatic area, nevertheless, show striking similarities, morphological and genetical, in comparison with the larger differences between races of the same subspecies from other climatic areas, such as coastal as compared with inland, and southern with northern races, for example.

As an example of a population of *typica* from a different climatic area, one from the northern inner Coast Ranges of California at Cobb, Lake County, may be compared with the populations from the more immediate coast at Montara

TABLE 2

Populations of Potentilla glandulosa from the central California transect as grown at Stanford

Subspecies, culture number, and origin	Number of plants		Mean date of first flowers in 1944	Longest stems, means (cm.)	Longest leaves, means (cm.)		Degree of winter activity
	Flowering	Non-flowering			Length	Width	
typica							
4060, Montara base, 60 m.	59	1	April 12	34.9 ± 0.6	21.3 ± 0.5	7.5 ± 0.2	active
4061, Montara summit, 275 m.	58	2	April 9	29.4 ± 0.7	20.0 ± 0.6	7.0 ± 0.2	active
3973, Montara summit (selfed), 275 m.	56	1	April 13	32.4 ± 0.7	19.0 ± 1.3	6.1 ± 0.5	active
3974, The Indians, 600 m.	3	..	April 10	24.3	....	....	active
3760, Cobb, 750 m.	37	1	April 20	45.4 ± 1.9	....	....	active
reflexa							
3976, Moccasin, 250 m.	58	..	April 9	60.8 ± 0.8	20.7 ± 0.7	6.6 ± 0.2	active
3977, Groveland, 910 m.	38	..	April 20	51.7 ± 1.4	19.3 ± 0.8	5.6 ± 0.8	short dormancy
3978, Hardin Flat, 1060 m.	59	..	April 21	57.9 ± 1.3	20.1 ± 0.6	5.7 ± 0.2	short dormancy
4064, Hetch Hetchy, 1190 m.	58	..	April 29	68.5 ± 1.8	25.8 ± 0.6	6.8 ± 0.2	short dormancy
4063, Mather, 1400 m.	57	1	May 5	56.4 ± 1.5	22.4 ± 0.6	6.4 ± 0.2	short dormancy
3979, Cottonwood Trail, 1650 m.	54	4	May 5	55.1 ± 1.3	19.1 ± 0.8	5.7 ± 0.2	short dormancy
hanseni							
4065, Mather Meadow, 1400 m.	20	40	June 5	37.3 ± 3.3	12.3 ± 0.4	5.5 ± 0.2	dormant
3980, Cottonwood Meadow, 1830 m.	27	28	May 20	43.3 ± 2.9	11.0 ± 0.5	4.9 ± 0.2	dormant
3981, Smith Meadow, 1950 m.	47	11	May 17	50.5 ± 2.1	13.3 ± 0.5	5.1 ± 0.2	dormant
3982, Aspen Valley, 1950 m.	2	34	June 10	37.5	7.8 ± 0.4	3.5 ± 0.2	dormant
3983, above Aspen Valley, 2040 m.	47	12	May 6	41.4 ± 1.6	10.1 ± 0.4	4.4 ± 0.1	dormant
4066, Middle Fork, 2100 m.	59	..	May 1	49.8 ± 1.1	10.0 ± 0.3	4.2 ± 0.1	dormant
3984, White Wolf, 2530 m.	45	..	April 26	41.9 ± 1.7	9.1 ± 0.4	4.5 ± 0.2	dormant
1096, Dark Hole, 2440 m.	6	..	April 28	41.0	....	....	dormant
4067, Yosemite Creek, 2190 m.	35	25	May 18	36.2 ± 1.9	8.5 ± 0.3	4.0 ± 0.1	dormant
1098, Porcupine Flat, 2470 m.	5	..	May 6	37.5	....	....	dormant
nevadensis							
4068, Tenaya Lake, 2590 m.	51	4	April 11	19.8 ± 0.9	6.9 ± 0.3	2.5 ± 0.1	dormant
4069, Tuolumne Meadows, 2740 m.	57	1	April 17	20.4 ± 0.9	7.5 ± 0.3	2.9 ± 0.1	dormant
4070, Dana Meadows, 2910 m.	22	1	April 16	17.3 ± 1.4	6.3 ± 0.5	2.5 ± 0.1	dormant
4071, Timberline, 3170 m.	52	1	April 5	18.7 ± 0.9	6.5 ± 0.3	2.3 ± 0.1	dormant
4072, Big Horn Lake, 3350 m.	46	2	April 15	15.6 ± 0.5	4.3 ± 0.2	1.6 ± 0.1	dormant

just described. Sample specimens of both are illustrated in figure 1. The more leafy and congested inflorescences of the Montara race and the wider, heavier-textured leaves are obvious differences. In the Stanford garden, Cobb flowers about 10 days later than Montara (table 2), and the two races show every evidence of being genetically fairly distinct, although they have many characters in common, including a normally active growth period during the winter months at Stanford, and numerous morphological characters. Although the Cobb population has not been tested by transplanting to the Mather and Timberline stations, we believe that it probably represents a recognizable climatic race, or ecotype, comparable in degree of differentiation with the Sierra Nevada southern foothill components of *typica* described in Volume I of this series.

The type collection of *Potentilla glandulosa* came from the Coast Ranges of northern California. As described in Volume I of this series, forms morphologically resembling the type of the species can be traced through the herbaria northward to Vancouver Island in British Columbia, southward to at least the northern boundary of Baja California, and eastward to the Great Basin areas of Washington, Oregon, Idaho, and California.

A territory of this size and climatic diversity is likely to be inhabited by more than a single geographic subspecies, and some of the northern and interior forms may be found to belong to new subspecies. Races from the Wallowa Mountains in northeastern Oregon classified as *typica* did not survive at Stanford but grew well at Mather (Clausen, Keck, and Hiesey, 1940, p. 61), and evidently are physiologically distinct from California coastal forms of *typica*. Probably several ecologically and physiologically distinct races are included in forms previously thought to belong to subspecies *typica*.

Another example is a race from Picture Gorge along the John Day River, northwest of Dayville, Grant County, Oregon. This form when collected in the wild was classified as subspecies *typica* because of its apparent morphological similarity, as seen on herbarium specimens, to forms of the species near the coast. When grown from seed in the Stanford garden alongside populations of *typica* from California, it proved to be strikingly different both morphologically and physiologically. The John Day plants had strictly erect, lemon-yellow petals that touched each other to form a narrow cylinder, in contrast with forms of *typica* from central California with openly rotate or ascending petals that were nearly pure white.

Physiologically, the contrasts between the races were even greater. In the Stanford garden the John Day plants, far out of their range and dormant during the mild winter, grew poorly and developed into highly variable, stunted to fairly vigorous plants that frequently died in the cultures, in contrast to the uniformly vigorous growth of all-year active central California forms in the same garden. Moreover, the John Day plants displayed striking modifications in the Stanford garden as compared with their appearance when collected in the wild. The Stanford-developed stems were thin, slender, and divaricate, and unlike the robust, erect stems developed in the native environment of the race.

Examples of individual variability within the John Day race, and differences between the John Day and Montara forms of *P. glandulosa,* are shown in figure 5. Races tend to exhibit greater individual variability when grown in an environment near their threshold of tolerance than when they are grown in an environment to which they are well fitted. In an unfavorable climate, small differences between individuals may determine success or failure, whereas a race

FIG. 5. Comparison of a race of *Potentilla glandulosa* subspecies *typica* from near the coast at Montara, San Mateo County, California, with three individuals of a race from the John Day River, 6 miles west of Dayville, Grant County, Oregon, grown in the same garden at Stanford. Herbarium specimens taken in 1944.

is likely to appear to be more homogeneous when it grows in an environment suited to all its individual variants.

The John Day race, which comes from a continental climate with severe winters, is winter-dormant at Stanford, whereas the California forms are strongly winter-active. Since the John Day race is so distinct from the California coastal forms of *typica,* both in morphology and in its growth responses, it obviously should be recognized as a separate subspecies.

Forms that properly belong to subspecies *typica* include races from the Rogue River and Grants Pass region in the Coast Ranges of southern Oregon, and

have been described in Volume I of this series (p. 61). The somewhat more successful growth of the southern Oregon plant at Mather as compared with Stanford indicates that there are minor physiological differences between these and plants from the Coast Ranges of central California.

Another ecological race of subspecies *typica* occurs in the Lake Tahoe region of the central Sierra Nevada at an altitude of 2700 m. Morphologically, it belongs to *typica,* but, unlike the Coast Range populations, it becomes winter-dormant at Stanford.

It is clear that the taxonomic subspecies *typica* of *Potentilla glandulosa* is of very complex composition. Individuals within each local population differ in minor but distinguishable morphological and physiological characters. Neighboring populations differ statistically in their average biotype composition even though they belong to the same ecotype. Populations from climatically distinct regions are to a greater degree divergent both morphologically and physiologically and represent separate ecotypes.

These kinds of variation are common to subspecies of many species. But the complex that has previously been considered to be *Potentilla glandulosa* ssp. *typica* is multiform to a special degree. Pockets of forms that in herbaria appear to be *typica* have established themselves over a large area extending over many climates. These finger in among other recognizable subspecies of *glandulosa,* but have nevertheless maintained a certain degree of morphological identity. Many evolutionary changes must have taken place within the *Potentilla glandulosa* complex in relatively recent geologic ages as the terrain of the Pacific states was sculptured and as many new environments arose providing diverse local habitats for new forms.

The morphological distinctness between the subspecies of *Potentilla glandulosa* tends to break down in areas where they meet and hybridize, and also in areas of topographic and edaphic complexity that provide microclimatic niches. Such intergradations, however, are not sufficient to erase the morphological identity of these subspecies.

Subspecies reflexa. This subspecies of the foothill regions is morphologically and physiologically distinct from *typica,* and it occupies a different ecological zone with a characteristic kind of climate. Subspecies *reflexa* is found on the warm, moderately dry western slopes of the Sierra Nevada from 250 to 2200 m. altitude, where it often is associated with *Pinus sabiniana* Dougl. and *P. ponderosa* Dougl., whereas *typica* is essentially a form of the cool, moist coastal areas. The morphological differences between *reflexa* and *typica* are summarized in table 1, and some of them are evident in figure 2. The subspecific name, *reflexa,* is descriptive of the recurved petals characteristic of the group. The plants of *reflexa* are densely pubescent but less prominently glandular than those of *typica.*

When individuals of *reflexa* are cloned and transplanted to the Stanford, Mather, and Timberline gardens, the ramets survive at Stanford and Mather;

they grow with greatest vigor at Mather, and fail to survive at Timberline. These general responses of *reflexa* are roughly parallel to those of the corresponding climatic race of *Achillea lanulosa* Nutt. from Groveland, as described in Volume III of this series (Clausen, Keck, and Hiesey, 1948, pp. 54, 67–72), but the *reflexa* forms extend over a greater altitudinal range than this single climatic race of *Achillea.*

The subspecies *reflexa* is, like *typica,* composed of varying elements. There are minor differences among individuals of each local population in the habit of growth, the length of the stems and leaves, the density of pubescence, the intensity of anthocyanin pigmentation, the size, shape, and color of the petals, and the degree of reflexion of the petals. Table 3 lists some of the intra- and interpopulation variations in floral and anthocyanin characters of this and other subspecies. Figure 3, page 8, shows the corresponding variation in leaf size at Stanford. Despite these variations, however, subspecies *reflexa* is a natural and easily distinguishable biological entity.

Within the altitudinal range of approximately 2000 m. covered by *reflexa* there are appreciable climatic differences. Correspondingly, there are distinct ecotypes within the subspecies. The Moccasin Creek population from the lower slopes of the Sierra Nevada at 250 m. altitude is as winter-active and as early-flowering at Stanford as *typica,* flowering 2 to 4 weeks earlier than plants of the winter-dormant forms of *reflexa* from 910 to 1650 m. There are, therefore, at least two ecotypes within subspecies *reflexa.* These differences in earliness and winter dormancy are indicated in table 2. Table 2 shows also that the mean stem lengths of *reflexa* populations from altitudes between 250 and 1650 m. ranged between 52 and 68 cm. Plants of *reflexa* from above 1700 m. were mostly shorter-stemmed, ranging between 30 and 64 cm. with a mean of 42.5 cm. (Volume I, p. 70, table 5).

Subspecies *typica* and *reflexa* both have a tendency to develop a branched crown consisting of short, woody stems, each branch ending with a rosette. These crowns grow a little higher each year, forming a dense cushion with the new spring buds 10 to 25 cm. above the ground level in older plants. The flowering stems develop from the rosettes at the apex of the woody crowns, and after the seeds ripen the flowering stems wither. In terms of Raunkiaer's classification of life forms (1934), these two subspecies are cushion chamaephytes, and the old leaves fill the space between the permanent, somewhat woody stem crowns. Figure 6 shows the stem crown of a plant of subspecies *reflexa* from Oak Grove, Tulare County, California, which had been grown at the Mather transplant station for a period of 8 years. In the same figure is also shown the root system of the rhizomatous subalpine form of subspecies *nevadensis.*

In summary, the forms of subspecies *reflexa* from the oak and digger pine woodland in the foothills can be considered to belong to an early-flowering ecotype that is winter-active when grown at Stanford, as contrasted with another ecotype from the ponderosa pine forest that is winter-dormant and is later in flowering. Within both ecotypes, considerable intrapopulation varia-

TABLE 3

VARIATIONS IN FOUR CHARACTERS WITHIN POPULATIONS OF POTENTILLA GLANDULOSA AT STANFORD

Frequencies indicate number of individuals within each class.

Subspecies and culture number*	Petal length (mm.)									Petal color						Petal orientation			Anthocyanin		
	4	5	6	7	8	9	10	11	12	Deep yellow	Yellow, bleaching	Cream-yellow	Cream	Cream-white	White	Reflexed	Horizontal	Upcurved	Green	± Antho-cyanous	Dark antho-cyanous
typica																					
4060	..	30	2	..	..	..	..	..	..	..	..	..	..	60	..	..	..	60	..	56	4
4061	..	11	12	..	..	..	..	..	..	..	..	..	..	58	..	..	28	30	31	6	..
3760	..	38	..	..	..	..	..	..	..	..	..	..	..	38	..	..	..	38	..	..	38
reflexa																					
3976	10	21	5	..	..	..	..	..	..	34	2	..	..	..	..	36	..	..	..	..	60
3977	..	..	..	..	..	..	..	..	..	20	8	..	..	..	..	22	6	..	..	9	20
3978	..	..	..	..	..	..	..	..	..	43	7	..	..	..	..	47	3	..	..	13	41
4064	..	..	12	22	12	..	..	..	..	30	16	..	..	..	..	31	14	..	24	6	29
4063	..	..	17	24	9	5	..	..	..	50	5	..	..	..	..	..	..	..	24	36	..
3979	..	4	9	22	12	4	..	..	..	37	14	..	..	..	..	17	30	..	..	51	..
hanseni																					
4065	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20	47	9	..
3980	..	..	..	2	1	6	6	5	..	..	..	1	6	7	6	..	..	59	45	14	..
3981	..	..	..	..	..	3	13	18	4	..	..	..	1	8	29	..	..	50	54	6	..
3983	..	..	..	..	4	13	17	8	3	..	3	15	17	7	3	..	..	45	52	7	..
4066	..	..	2	2	3	22	18	9	..	..	..	1	16	5	36	..	..	58	58	..	..
3984	..	..	..	1	..	4	13	13	10	..	..	8	22	7	4	..	..	45	47	1	..
1096	..	..	..	..	..	..	1	4	1	..	..	..	4	2	..	..	..	6	2	4	..
4067	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	35	49	5	..
1098	..	..	..	..	1	2	2	..	..	..	..	..	5	..	..	..	..	5	1	4	..
nevadensis																					
4068	..	..	..	1	2	12	18	8	10	..	..	2	6	19	24	..	..	51	57	..	..
4069	..	..	..	5	8	18	14	9	1	..	..	13	25	15	2	..	..	55	57	..	..
4070	..	..	..	1	8	8	3	..	..	..	..	5	11	4	..	1	19	..	26	..	..
4071	..	..	1	1	18	13	14	3	1	..	..	3	20	18	10	..	..	53	53	..	..
4072	..	..	1	12	19	13	1	..	..	..	..	1	12	14	19	..	..	46	46	..	..

* For origin of cultures see table 2.

Fig. 6. Root and crown systems of subspecies *nevadensis* and subspecies *reflexa*.

Above: Portion of plant 1113-10, subspecies *nevadensis*, above Slate Creek Valley, Mono County, California, at 3300 m. elevation, after having been grown for 18 years in the transplant gardens at Mather.

Below: Plant 1127-1, subspecies *reflexa*, from Oak Grove, Tulare County, California, at 750 m., after having been grown for 8 years in the transplant gardens at Mather.

tion, and also some differences between populations, are found, although below 1700 m. there is scarcely a definite altitudinal trend. Frequency diagrams of the variations in heights of flowering stems at Stanford of the various *reflexa* populations from altitudes of 250 to 1650 m. are shown in figure 7. The diagrams indicate no significant trends of plant height in relation to altitude.

SUBSPECIES HANSENI. Although the distribution of *reflexa* and *hanseni* overlaps markedly at middle altitudes in the Sierra Nevada, the two can be readily distinguished through a combination of morphological and ecological characteristics. As compared with the spreading stems, divaricate, open inflorescences, and narrow, yellow, reflexed petals of *reflexa, hanseni* has rigidly erect stems with compact inflorescences, wider, cream-white, upcurved petals, less pubescence, and leaves with somewhat shorter petioles. Moreover, *hanseni* produces fewer flowering stems at Stanford than *reflexa,* and it flowers 3 to 4 weeks later than forms of *reflexa* from the same altitudes.

The subspecies *hanseni* is one of the most variable of the four from the central California transect. Table 3 indicates how the Stanford-grown individuals of each of the populations vary in certain floral characters and in degree of anthocyanin. It will be seen from figures 3 and 4 that the leaflets of *hanseni* produced at Stanford are more crowded than those of *reflexa,* and have shorter petioles. At Stanford, but not in its native habitats, the leaflets of *hanseni* are usually somewhat overlapping, although some individuals have as well separated leaflets as *nevadensis.*

Table 4 lists the individual variability within each population in length and width of longest leaf. In this character there is no evident correlation with altitude in the range covered by the subspecies, namely, from 1400 to 2530 m. altitude. The three populations from 1400 to 1950 m. have the largest leaves, but another population from 1950 m. altitude, 3982, has the smallest. That culture came from an area having only a few individuals in a small, isolated meadow. The small size and isolation of this population would favor reduced variability and distinctness from other populations within the same general area.

Strains from near the center of the distribution of the subspecies flower most abundantly at Stanford and are also among the earliest, as is indicated in table 2. On the other hand, plants from the upper range nearer the area of *nevadensis* flower less abundantly and approximately 3 weeks later than those from the center. The Mather population from the lower altitudinal zone of *hanseni* is the latest to flower, has the fewest stems when grown in the garden at Stanford, and borders on being a distinct ecotype within the subspecies.

Despite the variation within it, subspecies *hanseni* is fairly local in the central Sierra Nevada, extending some 125 miles from south to north in a narrow zone only about 30 miles wide. Characteristic for *hanseni* is its lateness of flowering, a trait common for many meadow species from middle altitudes, and very sparse flowering when grown at Stanford, in contrast with the freely flowering subspecies *reflexa* and *nevadensis.* Coastal *typica,* being bounded on one side by the ocean, is less exposed than *hanseni* to the influx of genes from other system-

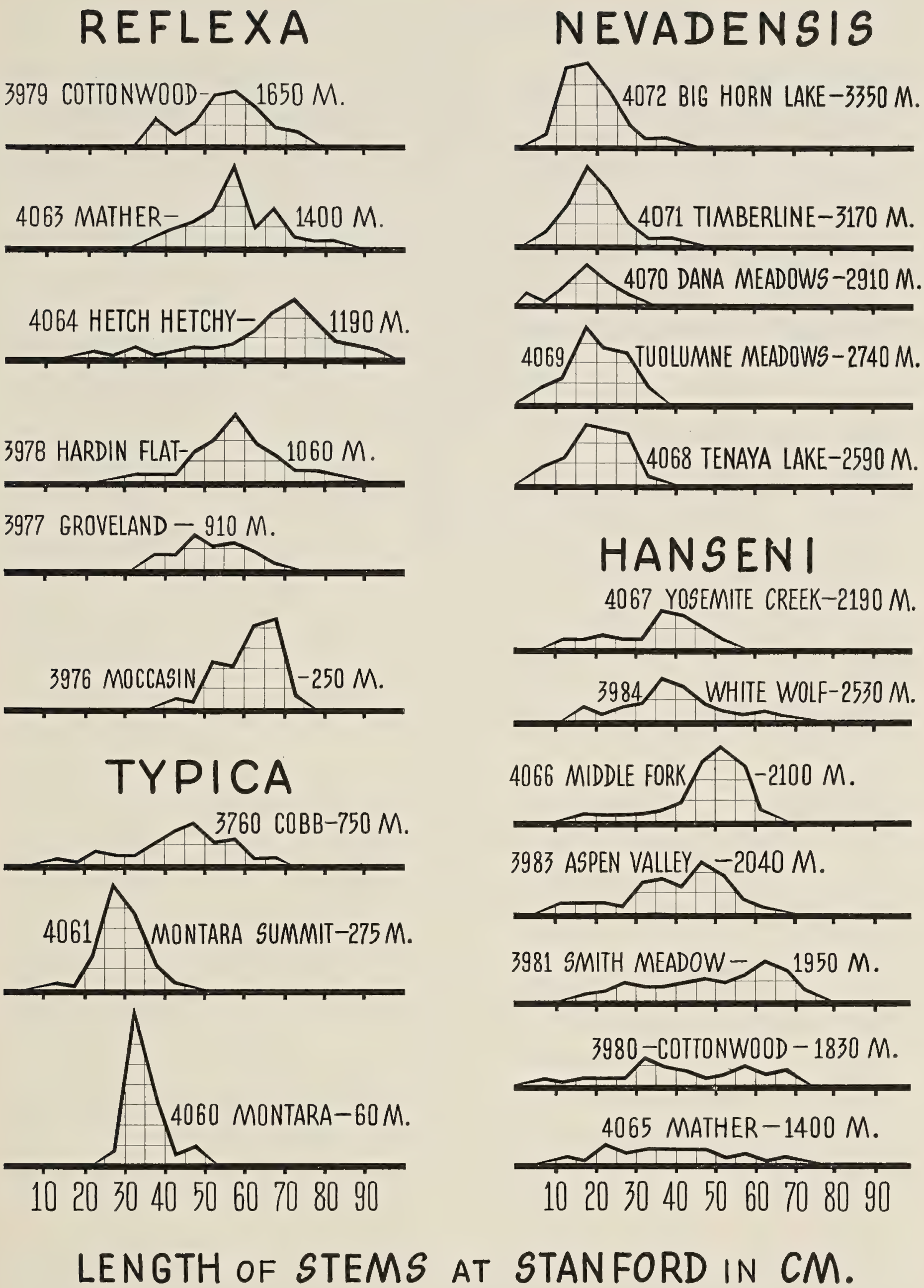

Fig. 7. Variation in length of stems of populations of *Potentilla glandulosa* originating from points along the central California transect and grown from seed in uniform conditions at Stanford. The frequency curves are based on measurements of the longest stem of about 60 individuals of each population during 1943 and 1944. In the horizontal direction each square represents 5 cm. of stem length, and in a vertical direction a frequency of 5 individuals. Measurements were made to the nearest centimeter.

See table 3 for further data on the same populations.

atic units of the species, and may for this reason show less genetic variation. Subspecies *hanseni* appears to have a relatively small gene pool of its own, but it is surrounded by other subspecies that may contribute to its variability.

Subspecies *hanseni* is especially significant from an evolutionary viewpoint because its forms constitute a link between the foothill and high-altitude races

TABLE 4

VARIATION IN LENGTH AND WIDTH OF ROSETTE LEAVES IN POPULATIONS OF SUBSPECIES HANSENI GROWN AT STANFORD

LONGEST LEAVES, CLASS RANGES (CM.)	CLASS FREQUENCIES IN POPULATIONS							
	4065 Mather, 1400 m.	3980 Cotton-wood, 1830 m.	3981 Smith Meadow, 1950 m.	3982 Aspen Valley, 1950 m.	3983 Above Aspen Valley, 2040 m.	4066 Middle Fork, 2100 m.	3984 White Wolf, 2530 m.	4067 Yosemite Creek, 2190 m.
Length								
3–5	..	..	1	3	..	1	1	1
5–10	12	19	7	*20*	*27*	24	*26*	*41*
10–15	*30*	*24*	*30*	5	22	*28*	14	12
15–20	13	5	14	..	1	1	..	..
20–22	..	..	1	..	..	..	..	..
Means	12.3	11.0	13.3	7.8	10.1	10.0	9.1	8.5
Width								
1–2	..	..	..	1	..	1	..	..
2–3	1	2	1	4	3	2	3	6
3–4	6	11	9	*17*	15	20	*13*	*22*
4–5	*21*	*14*	*19*	6	*21*	*22*	*13*	*22*
5–6	12	13	12	..	7	7	8	3
6–7	5	6	9	..	4	2	3	1
7–8	7	1	3	..	..	..	1	..
8–9	3	1	..	..	..	..	..	..
Means	5.5	4.9	5.1	3.5	4.4	4.2	4.5	4.0
Totals	55	48	53	28	50	54	41	54

of the subspecies *reflexa* and *nevadensis*. The populations of *hanseni* from near the zone of *nevadensis* contain plants that have leaf shapes similar to those of *nevadensis* (fig. 4), although they still are wider (table 2). Similarly, the size of the petals, the general degree of flowering, and earliness tend to increase in populations from higher altitudes, whereas pubescence decreases. With increasing altitude, therefore, *hanseni* tends more and more to resemble *nevadensis*. Nevertheless, even the populations that geographically are the closest to *nevadensis* are still morphologically distinct from it.

The same trend is seen in the life form. The forms of *hanseni* are generally hemicryptophytes, that is, their regenerating spring buds arise at the surface of the ground; the *hanseni* populations from lower altitudes, however, develop short woody crowns similar to the chamaephytes of *reflexa,* whereas those from higher altitudes are more rhizomatous, as in *nevadensis* (cf. fig. 6).

The morphological resemblance of certain forms of *hanseni* from higher altitudes to *nevadensis* caused the writers previously to include the Dark Hole and Porcupine Flat populations of *Potentilla glandulosa* with *nevadensis* (Clausen, Keck, and Hiesey, 1940, p. 84). More extensive sampling and the morphological study of mid-altitude populations in the transplant gardens indicate that these two populations belong with *hanseni* rather than with *nevadensis.* This later interpretation of *hanseni* leads to a more natural morphological, ecological, and physiological concept of the two subspecies.

In the Stanford garden, the seedling plants of *hanseni* develop characteristic rosettes bearing short, wide, heavy-textured leaves that grow slowly and remain wholly vegetative the first 2 years. During the third and later years they develop a few strictly erect flowering stems with compact inflorescences, but flowering is always sporadic at Stanford, and many individuals remain vegetative whereas others flower freely in certain years. By contrast, the seedling populations of subspecies *nevadensis* flower consistently and freely during the second year at Stanford.

At all three stations the individuals of *hanseni* are among the latest of all forms of *Potentilla glandulosa* to flower, and the forms of *nevadensis* are the earliest. Thus, although the forms of subspecies *hanseni* and *nevadensis* may approach each other morphologically in their native environments, they respond very differently when compared in the same environment. Physiologically, therefore, they are fairly distinct.

Even more marked are the differences in survival at the stations between the subspecies *hanseni* and *reflexa.* Both thrive at Mather, but at Timberline *hanseni* survives consistently, whereas *reflexa* does not, and at Stanford *reflexa* survives and grows better than *hanseni.*

The mid-altitude meadow subspecies *hanseni* is a small evolutionary complex that has great potential variability. Tendencies toward distinct ecotypes are clearly recognizable, but as yet these do not appear to have become completely differentiated.

Subspecies nevadensis. In the transect across central California this subspecies is confined to the highest ranges of altitude in the Sierra Nevada, the zone occupied by forests of *Pinus murrayana* Balf. and *P. albicaulis* Engelm. A series of morphological and physiological characteristics distinguishes this form from the other subspecies, but it is most closely related to *hanseni.* It produces a root system with extensive slender underground rhizomes whose terminal buds reach the surface of the ground and in spring give rise to a new crop of rosette leaves and flowering stems as shown in figure 6. According to the classification of

Raunkiaer (1934), it is a hemicryptophyte. The leaves are smaller and more glabrous than those of the other subspecies; the stems are slender, short, and mostly strictly erect, and they bear flowers with large cream to white upcurved petals that prominently exceed the sepals.

Subspecies *nevadensis* typically inhabits south-facing, sunny, moist, rocky slopes and meadows and usually grows in good loam soil in pockets of rock crevices, along silted streamways, or in well drained meadow areas. Its altitudinal range is from 2500 to 3300 m., its upper limit extending somewhat above tree line. Plants of *nevadensis* from this range of altitudes are illustrated in figure 2. Subspecies *nevadensis* occurs in a higher altitudinal belt than *hanseni;* the ranges of these two subspecies do not appear to overlap in altitude, and in places there appears to be a gap in the distribution of the two. Further sampling, however, may disclose populations of both subspecies in close proximity. An airline distance of approximately 5 km. separates the nearest colonies observed by the writers in the Yosemite National Park area.

Seedling cultures of *nevadensis* grow moderately well at Stanford for 2 or 3 years, but never attain the vigor of subspecies *typica,* which is at home in this environment. In contrast with *typica* and *reflexa,* seedlings of *nevadensis* develop slowly the first year, and about half of the plants produce flowers the second year. Their peak in vigor at Stanford is attained during the third year, when most seedlings flower freely—much more so than plants of *hanseni* ever do in this environment, as is shown in table 2. Cloned transplants of *nevadensis* thrive much better at Mather and at Timberline than at Stanford. At the alpine station all forms of *nevadensis* flower consistently, and most of them succeed in ripening some seed even during the shortest summer. Of all the subspecies, *nevadensis* is the only one that is truly successful at Timberline.

Plantings of *nevadensis* at Stanford from seeds collected in five wild populations over a range of 750 m. of altitude have been studied, and some of their characteristics are described in table 3. The class frequencies listed in the table indicate that *nevadensis* is probably the least variable of the four subspecies. The fact that the populations from the highest altitudes have the most regular frequency curves suggests that the more rigorous selection at these altitudes may eliminate all but a narrow range of biotypes and thereby reduce the genetic variability within the population.

There is no lack of variability within *nevadensis,* however, for, as in other subspecies, appreciable differences are found among individuals in such characters as the size and shape of the basal leaves, as illustrated in figure 4. Color of petals (table 3) varies from white to cream-yellow, and size and shape of petals differ among individuals.

There are also differences among populations in their composition of biotypes. Some of the interpopulation differences appear to be correlated with altitudinal gradients; others do not. For example, white-petaled individuals are much more common at Tenaya Lake and Big Horn Lake, the lower and upper limits, respectively, of the subspecies, than at intermediate localities (table 3). Neverthe-

less, the alpine population from Big Horn Lake stands out as ecotypically distinct from the others, with significantly shorter stems and smaller leaves, and at Stanford it remains winter-dormant for a longer period than populations from lower altitudes.

In table 5 are listed the lengths and widths of rosette leaves of five populations of *nevadensis* from the central California transect when grown at Stanford. The figures indicate the variation for this character within each population, and show especially the tendency for the plants of the Big Horn Lake population to have

TABLE 5

VARIATION IN LENGTH AND WIDTH OF ROSETTE LEAVES IN POPULATIONS OF SUBSPECIES NEVADENSIS AT STANFORD

Longest leaves, class ranges (cm.)	Class frequencies in populations				
	4068 Tenaya Lake, 2590 m.	4069 Tuolumne Meadows, 2740 m.	4070 Dana Meadows, 2190 m.	4071 Timber-line, 3170 m.	4072 Big Horn Lake, 3350 m.
Length					
2–5	8	5	7	11	*27*
5–10	*33*	*44*	*10*	*38*	11
10–15	4	5	..	3	..
Means	6.9	7.5	6.3	6.5	4.3
Width					
0–1	..	..	..	1	1
1–2	11	6	5	14	*29*
2–3	*25*	*36*	*10*	*31*	5
3–4	9	11	2	4	..
4–5	..	1	..	1	..
Means	2.5	2.9	2.5	2.3	1.6
Totals	45	54	17	51	38

the smallest leaves. These are in rather abrupt contrast with the near-by Timberline population from an altitude only 250 m. lower, which falls in the same range of variation as other populations of *nevadensis* from lower altitudes.

It appears that subspecies *nevadensis* from the central Sierra Nevada contains at least two distinguishable climatic races, or ecotypes: an alpine, represented by the Big Horn Lake population; and a subalpine, which includes the other forms, ranging from Tenaya Lake to Timberline. It is probable that *nevadensis* from other latitudes in the Sierra Nevada, and from more southern mountain ranges such as the San Jacinto and San Bernardino Mountains, as well as the more northern Cascades and Blue Mountains of Oregon and Washington, have ecotypes that parallel those of the central Sierra Nevada.

Intergrades between subspecies. The subspecies of *Potentilla glandulosa* are most clear-cut in central California, where the valleys and mountain ranges parallel the coast line, and where the Sierras are high and unbroken by low passes. Here the climatic zones replace each other in a fairly clear-cut series, and the selective influence of contrasting climates has produced distinct subspecies and ecotypes. Nevertheless, even here a considerable degree of intergradation occurs.

Toward the north, where the Sierra Nevada becomes progressively lower and more interrupted through a merging with the Siskiyou and Cascade Ranges, the environments show less contrast. The relatively clear-cut zones that follow along the contour lines of the central Sierra Nevada fan out and merge with other climatic influences from the north, west, and east, and bring together floral elements from different regions. These reflect the complexity of the environmental influences that govern natural selection.

Plants referred to subspecies *typica* from this northern region, for example, were previously grown in our transplant experiments (Clausen, Keck, and Hiesey, 1940, table 3, p. 60). They were from Grants Pass, Josephine County, and from the Rogue River region in Jackson County of southern Oregon, and had light yellow petals instead of white, and openly divaricate branching rather than erect and compact, characters of subspecies *reflexa*. Most of their characters, however, such as large sepals, fleshy receptacles, nonreflexed petals, and dark-colored akenes, were those of *typica*.

The rise of the California Coast Ranges greatly changed the climate in the interior and provided new environmental niches. It is possible that present-day *reflexa* and *typica* evolved from an original intermediate stock in response to the new opportunities. There is no evidence, however, to indicate the exact evolutionary course that has been followed.

South of the present-day Central Valley of California the Sierra Nevada is replaced by the Tehachapi Mountains, which run east and west and link the Coast Ranges with the Sierra Nevada. In this region, and in the topographically complex ranges of the San Gabriel, San Bernardino, San Jacinto, and other mountains of southern California, the rather well defined subspecies found in central California break down into other combinations of characters as the effects of a more southern latitude are added.

In many situations in the Sierra Nevada two subspecies of *Potentilla glandulosa* occur adjacent to each other. This is especially true at mid-altitudes, where *hanseni* grows in the moist meadows, and *reflexa* on the adjacent warmer and dry slopes. The inclination is to interpret the variation seen within each of these ecologically distinct populations as having arisen through recent hybridization. It must be remembered, however, that neighboring populations of these two subspecies may differ in time of flowering by as much as a month. Also, the study at Stanford of 60 seedlings per population grown to maturity rather emphasized the physiological distinctness of the subspecies and the scarcity of hybrids. A natural hybrid between two subspecies was described in Volume I (p. 52, fig.

16), taken at 1680 m. altitude on the western slope of the Sierra Nevada at Ockenden, Fresno County, California. This locality was populated by true *reflexa* on the dry slopes, forms of *hanseni* in a meadow, rare individuals of *nevadensis,* and also individuals that appeared to be hybrids.

Undoubtedly, at the edges of the distribution of the four subspecies of *Potentilla glandulosa* a certain amount of hybridization is constantly taking place. Natural selection, however, limits the extent of genic infusion among the subspecies. In regions where equilibrium has thus been reached, the subspecies are able to maintain their identity. Where environmental zones differ because of the confluence of topographic features, changes in soils, climate, or biotic factors, selection from the available gene pool may shift in a new direction. It is primarily the physiological rather than the morphological characteristics that govern the course of selection, and classifications according to morphology may conflict with the ecological evidence.

The morphologically fairly distinct ecologic subspecies of *Potentilla glandulosa* are in contrast with the less distinct subspecific categories in the *Achillea millefolium* complex. In *Achillea borealis* and *A. lanulosa* the extreme forms differ so markedly that they can readily be recognized, but the intermediate races defy acceptable taxonomic resolution of the variability into other subspecies further than *arenicola* (Heller) Keck of the coastal dunes and bluffs, *californica* (Pollard) Keck of the Coast Ranges and foothills, and *gigantea* (Poll.) Keck of the Central Valley, all belonging to *A. borealis.* In *A. lanulosa,* subspecies *typica* and *alpicola* (Rydb.) Keck can be recognized, but the contiguous ecotypes of *A. borealis* and *A. lanulosa* cannot be distinguished with certainty from each other except through their chromosome numbers. In *Potentilla glandulosa* the four subspecies can usually be identified in central California, but a certain fraction of intermediates complicate the classification.

In both *Achillea* and *Potentilla* the contrasting races doubtless represent species in the process of being evolved; in *Potentilla* the trend is toward a number of distinguishable but closely related ecospecies, but in *Achillea* future development of barriers to free interbreeding will probably not result in morphologically recognizable taxonomic species. At present we are apparently witnessing the early stages of speciation along two different patterns in these two groups.

Conclusions concerning the composition of Potentilla glandulosa. This widespread species is clearly composed of many contrasting races and myriads of biotypes whose differences are controlled by heredity. The differences range from the scarcely describable minutiae distinguishing two similar individuals of one population to spectacular contrasts that have repeatedly led to descriptions as distinct species. All these have evolved on the diploid level with the simple basic set of 7 pairs of chromosomes. This multiplicity of forms does not occur at random, but in recognizable sequences that are definitely correlated with differences in the environment, especially the climate.

The first and lowest level of variability is found among individuals within a local population. The biotypes within the local population may have differential selective value under certain conditions, but all are sufficiently in harmony with their current habitat to enable them to survive with approximately equal success.

The second step in variability is that between isolated local populations occurring in one general climatic region and under about the same edaphic conditions. Such populations grown in the same standard environment frequently show statistically significant differences for certain characters, but these differences are of a random kind. In all traits, however, there is a wide margin of overlap in the variation between individuals of one population and the next.

A third step in differentiation occurs between populations growing in regions that are climatically different, or in habitats that are edaphically distinct. These differences are primarily physiological, and they become evident when such populations are grown in one environment or when their individuals are cloned and tested in contrasting environments. They are differences of distinct ecotypes, and may or may not be accompanied by morphological differences. If not, the ecotypes cannot be recognized in the wild because the environment compensates for physiological differences in growth responses.

The taxonomic subspecies of *Potentilla glandulosa* represent a fourth step in differentiation, and are morphologically so well marked that they can usually be recognized in the field. They are also ecologically so distinct that they occur in distinct climates. Each of the four subspecies along the central California transect contains at least two climatic races, or ecotypes.

The overlapping variation between these levels of differentiation, and the ability of each of the subspecies to hybridize with the others, produces a complex biological structure with sufficient physiological flexibility to compensate for the diversity of the natural environment.

Despite this wealth of variability, *Potentilla glandulosa* has not been able to produce races that fit all the available climatic niches in the area studied, for it is absent on the dry eastern slopes of the Inner Coast Range, in the hot arid San Joaquin Valley, and in the severe and continental climates of the Great Basin. It is therefore not as versatile as members of the *Achillea millefolium* complex discussed in Volume III of this series, but its ability to produce forms fitted to a great range of conditions is nevertheless wider than for most species of higher plants.

Figure 8 provides in diagrammatic form a summary of the interpopulation analysis of the sampled natural populations of *Potentilla glandulosa* along the central California transect. Mean data on stem height, dates of first flowers, and winter activity of 24 populations grown at Stanford are grouped according to subspecies and geographical sequence from the Pacific coast eastward to the summit of the Sierra Nevada. The diagram shows that a character such as winter activity at Stanford does not follow the morphological subspecies, but rather the altitudinal transect. The *reflexa* population from 250 m. altitude, for example, like the Coast Range *typica,* is winter-active at Stanford.

Considerable discussion in recent years has centered on the question whether intraspecific variation is continuous, or discontinuous with breaks at certain critical points in the natural distribution. Variations of single characters have usually been considered rather than combinations of characters of the kind that usually distinguish natural populations. Also, observations have rarely been made in a uniform environment where modifications can be distinguished from hereditary variations. The sampling has usually not been adequate to distinguish between truly continuous variation and essentially discontinuous variation that may be considered as a series of terraces connected either by steep slopes (i.e., a few variational forms) or by cliffs (actual discontinuities). Although the sam-

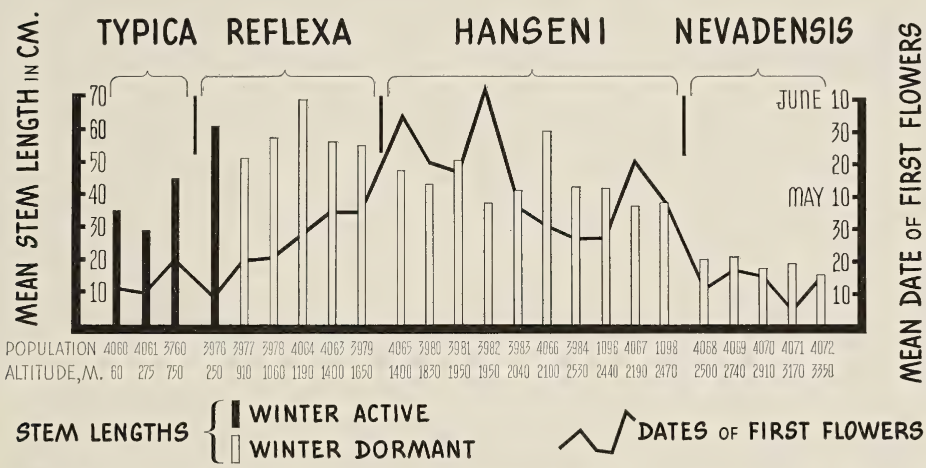

FIG. 8. Summary of average stem lengths, flowering time, and winter activity of populations of *Potentilla glandulosa* from the central California transect grown in a uniform garden at Stanford. The subspecies are indicated above the braces.

pling of *Potentilla glandulosa* along the transect of California has not been adequate to settle this problem conclusively for that species, the data available on 24 populations cover this transect fairly evenly and provide critical data on the question.

The curve in figure 8 indicating the mean date of first flowering within each population shows that the winter-active populations from the Coast Ranges and the low foothills are early. So also are all the highly winter-dormant populations of *nevadensis,* which develop rapidly as temperatures rise in early spring. The populations of *reflexa* follow a cline, being later in flowering with increasing altitude of origin. This trend is not followed, however, in populations of *hanseni,* which appear to vary at random for this and other characters. The diagram also indicates the marked difference in earliness of populations from 1400 m. altitude of *reflexa* as compared with *hanseni* from the same altitude, and the equally abrupt difference between *hanseni* from 2470 m. and *nevadensis* from 2500 m.

There are no continuous trends within the subspecies with regard to mean heights of stems, but rather a random variation from population to population. Other intrasubspecific variations probably reflect differences in the relative prevalence of various biotypes colonizing a given habitat, a phenomenon to which the terms "random fixation" and "genetic drift" have been applied. In comparing subspecies at Stanford, it is evident that *nevadensis* has distinctly shorter stems than *hanseni,* and that the stems of *typica* are shorter than those of *reflexa.*

In *Potentilla glandulosa* there appears to be both continuous and discontinuous variation. A complete intergradation, or cline, occurs for one character within one subspecies, whereas other subspecies appear to show random variation for the same character. Further study would probably multiply such examples of degrees of discontinuity and degrees of intergradation among the various ranks of natural entities.

II

GENETICS OF ECOLOGICAL RACES

The complex racial composition of *Potentilla glandulosa* as outlined in chapter I suggests that the genetic structure of this far-flung species is also complex. In an analysis of the genetic structure of such a group of forms it is more advantageous to attempt crossings between the most contrasting climatic races of the most distinct subspecies than to hybridize races whose characters overlap greatly. In this way a few crosses between key forms may be made to yield a great deal of information regarding the genetic structure of the species as a whole.

MATERIALS AND METHODS

THE RACES CROSSED. Four principal crosses have been studied in *Potentilla glandulosa,* as indicated in the diagram, figure 9:

1. A cross between a form of subspecies *nevadensis* from Upper Monarch Lake, Tulare County, at the crest of the southern Sierra Nevada at 3240 m. altitude, with a form of subspecies *typica* from the California coast near sea level at Santa Barbara. The F_1 and a large F_2 population of this hybrid were grown at Stanford.

2. A cross between the Santa Barbara coastal form of subspecies *typica* and a foothill form of subspecies *reflexa* from Oak Grove, Tulare County, growing in the chaparral belt at 760 m. elevation. An F_1 but no F_2 progeny were grown at Stanford.

3. The alpine form of *nevadensis* from Upper Monarch Lake crossed with the Oak Grove form of *reflexa.* Only F_1 plants of this cross were studied.

4. A cross between a subalpine form of *nevadensis* from Slate Creek Valley near the Timberline transplant station of the Carnegie Institution on the east flank of the central Sierra Nevada at 3050 m. altitude and the Oak Grove form of *reflexa.* F_1, F_2, and F_3 progeny have been grown and studied at Stanford. In addition, 578 F_2 individuals were cloned and grown simultaneously at the Stanford, Mather, and Timberline transplant stations, and their performance in these different climates was studied over a 5- to 9-year period.

Illustrations and brief descriptions of the parents and F_1 hybrids of three of the above crosses were given in Volume I of this series (Clausen, Keck and Hiesey, 1940, pp. 114–124), and preliminary accounts of the widely segregating F_2 of the fourth cross have also been presented (Clausen, 1949, 1954*a*). Since the 1940 report was written, much detailed study has been devoted to the F_2 progeny of the first and last crosses mentioned above, and the F_3 of Oak Grove × Timberline. The present chapter deals primarily with the analysis of these detailed studies.

GENERAL METHODS. In making the crossings, the parents were isolated in greenhouse cages and the flowers were emasculated. Reciprocal pollinations

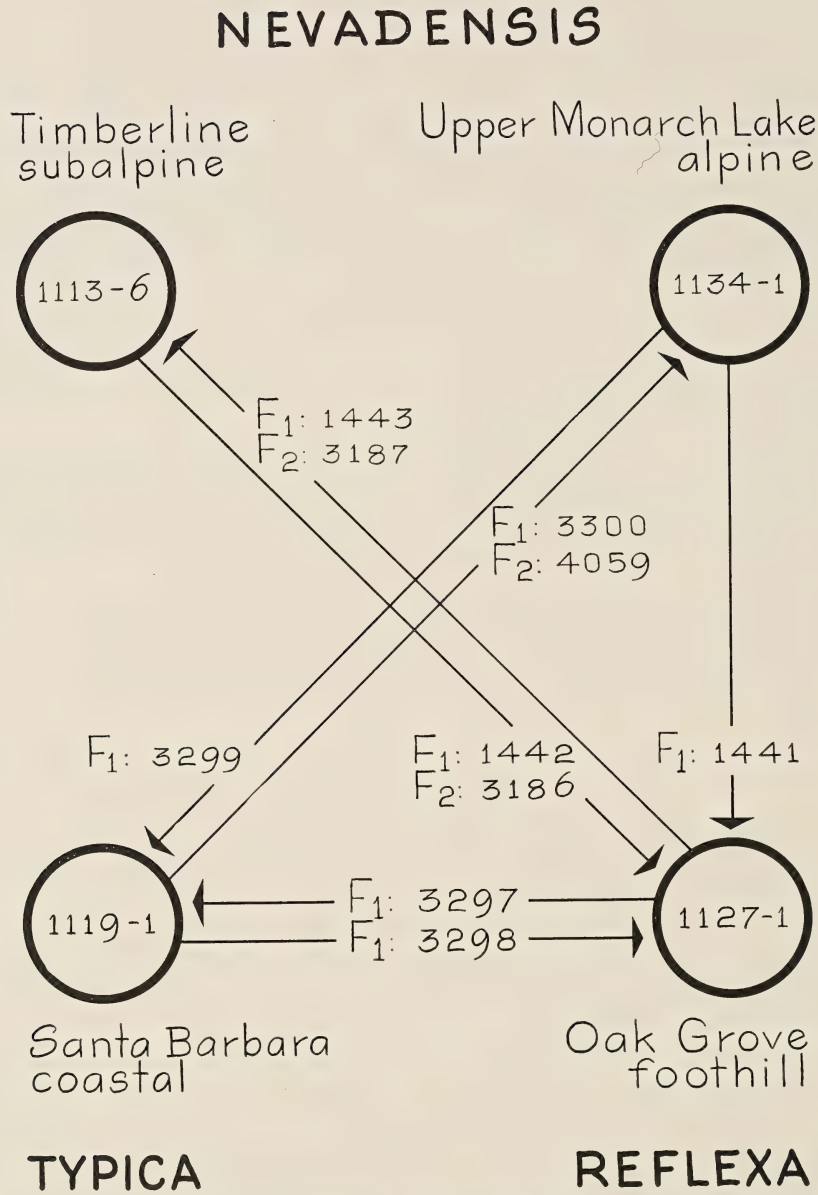

FIG. 9. Crosses between climatic races of *Potentilla glandulosa*. The numbers in circles refer to individual parent plants; those along the arrows, to culture numbers of the F_1 and F_2 progeny. The boldface lettering indicates subspecies.

were made, resulting in each instance in reciprocal F_1 progeny. All the parents and selected F_1 individuals of Timberline × Oak Grove and Upper Monarch Lake × Oak Grove were cloned and grown simultaneously at the Stanford, Mather, and Timberline transplant stations over a period of years, as reported in Volume I. The 41 F_1 progeny resulting from the cross Upper Monarch Lake × Santa Barbara and reciprocal were observed at Stanford between 1937 and 1944, and 1015 F_2's between 1942 and 1944.

In the cross Timberline × Oak Grove, 6 F_1 individuals (3 of each reciprocal) have been in culture and under experimental observation at Stanford and at the field transplant stations from 1934 to 1954. The 578 F_2 progeny resulting from self-pollinating 2 F_1 individuals (1 of each reciprocal) were grown as seedlings in the garden at Stanford in 1935, and each individual was then cloned into at least 3 divisions during 1937.

In 1938 one ramet (propagule) of each individual was planted at each of the transplant stations at Stanford, Mather, and Timberline. The sets of clones at the three stations were studied closely for 5 years, until 1943; in 1944 the Stanford planting was removed to make room for new experiments, but the Mather and Timberline plantings have been maintained until the present writing (1956) and have been observed during these years. Chapter III is devoted principally to an analysis of the responses at the three transplant stations of this F_2 population.

In 1940 a number of selected F_2 individuals of Timberline × Oak Grove were self-pollinated in cages; the F_3 progenies from these were grown in the Stanford garden and studied during the years 1942 to 1945 and have contributed to the study of the genetic basis of selected characters that distinguish the climatic races of *Potentilla glandulosa.*

Detailed measurements, tabulations, and written notes of the cultures were made throughout the investigation. In the study of the cloned F_2 of Timberline × Oak Grove grown at the three transplant stations, data on each clonal division of each individual were assembled on separate sheets on printed forms. Observations made by one investigator were frequently checked by another, and similar sets of observations were repeated during successive years. The final analysis of the results was based on mean values obtained by averaging the data from 4 years' observations at Stanford and 7 years' at Mather and Timberline. In this way a fair representation of the expression of each plant in each environment could be obtained.

In addition to these written records, sets of full-length herbarium specimens were preserved to supplement the data. Photographs made in the gardens of some of the plants further added to the completeness of the record.

The full description of individual plants in garden cultures, especially of highly segregating F_2's, required observations to be taken at different times of the year. In the F_2 of Monarch Lake × Santa Barbara these data were placed on labels beside each individual plant in the garden marked with the number of the plant. As new characters came to expression during the year they were

added to the labels. At the end of the year the labels were collected and filed as part of the record.

USE OF PUNCHED CARDS IN ANALYSIS OF DATA. The systematic study of the numerous data from many individual plants from different points of view presented a complex problem in statistical analysis. In order to interpret with full effectiveness the data on the genetic segregations and the environmental modifications of the characters of the F_2 offspring, it was necessary to make many kinds of comparisons. For some of the more complex problems, especially the analysis of genetic correlation in the two highly segregating F_2 populations, the work was greatly facilitated by means of punched cards sorted and tabulated by electrically operated machines.

This and other punched card methods have been used by biologists in dealing with various problems, but in each specific case the utilization of such mechanical aids requires some special study. Principles underlying the application of the electric punch card method to scientific computations have been outlined by Eckert (1940), and are elaborated further by Casey and Perry (1951). We shall describe here only details applicable to the present investigation.

The IBM cards used by the International Business Machines Corporation, also known as Hollerith punched cards, are 3¼ inches wide and 7½ inches long and accommodate 80 numbered vertical columns of figures. Each vertical column consists of the ten arabic numerals 0 to 9, and the vertical and horizontal numbers are aligned.

A special machine is used to punch rectangular holes at positions occupied by the desired numerals. Any data that can be coded in terms of numerals can thereby be transferred to the card. After the cards have been punched, they can be classified, by an electrical sorting machine, into groups according to any selected character that has been coded on the cards. The machine sorts the cards at the rate of 20,000 per hour, so that only 3 minutes are required to sort a pack of 1000 cards representing 1000 plants into as many as 13 different classified groups.

The sorting machine is controlled by electrical contacts made through the holes punched in the cards as they pass through the machine. A counting device records the number of cards sorted into each classified group. In the *Potentilla* analysis the sorting machines were particularly useful for obtaining the data needed for computing the correlation coefficients between all combinations of character pairs. Also, index values may be computed from these data, from which such graphs as are shown in figures 12 and 17 can be constructed.

The coding of the essential information from each individual plant into a form that can be transferred to punch cards requires careful study and organization of the data. It is essential that the information be tabulated in the form of a code of numbers. The sorting is much simplified if the number of classes into which a given character is subdivided is limited to 10 or less.

For each character the classes listed in tables 9 and 12, pages 40 and 50, provided the basis for the coding of the data on each plant. One vertical column on the punch card was assigned to each of the characters listed in the tables, and the columns appear in the same order as the characters in the tables. The class value of each character indicates its degree of expression and provides the code numeral.

An example will serve to illustrate how the description of a given plant was transferred to a punched card. The F_2 plant no. 257 of the cross Upper Monarch Lake × Santa Barbara, which is illustrated in figure 11 (upper row, extreme right), is described in terms of class values for each of the characters listed in table 9. The number of the plant, and the class values describing the degree of expression of each character, are listed in designated columns on a code sheet, as shown in table 6. After the data from all the F_2 plants of a population have been thus posted on code sheets, the cards are punched by a trained operator, each card representing an individual plant.

The punched cards are listed by a machine which prints all the numbers that have been punched on each card on a sheet of paper. In the present study the listed numbers were proofread back to the original code sheets to check against errors. The code sheets were prepared by the authors, but the punching of cards, listing, and sorting were done under contract with the International Business Machines Corporation in the Service Department of their San Jose, California, plant.

The reader is referred to table 44 for an example of the form in which data from an entire F_2 population may be prepared for punching on cards. Such coded forms can also be used as a means of recording a large amount of detailed information in relatively little space.

One of the aims in the present analysis was to list the frequencies of each combination of characters. Another was to determine whether characters that segregate in the F_2 populations are genetically correlated to a statistically significant degree. The first step in the solution of these problems was to prepare tabulations showing the number of plants falling into the various classes with respect to given pairs of characters. These tabulations were obtained with the aid of the sorting machine.

A sample tabulation of this kind is shown in table 7, in which the degree of winter dormancy in the Stanford garden is tabulated against the lengths of leaves. In the first sorting the entire pack of cards representing the whole F_2 population was sorted into the 6 classes of winter activity at Stanford, Do_1 to Do_6. Each of these 6 classes was, in turn, sorted separately into 8 classes according to leaf length, Ll_1 to Ll_8. The number of cards in each of the 48 groups was tallied by the automatic counters on the machine that furnished the data needed to fill the tabulation. A total of seven sorting-machine operations was therefore necessary to obtain the data for table 7.

To guard against machine errors, the sum of the group counts made by the separate counters was checked with the tally of the total number of cards passed

TABLE 6

CODING OF DATA FROM PLANT NO. 257 OF THE F_2 PROGENY OF UPPER MONARCH LAKE × SANTA BARBARA

Characters	Plant number				Inflorescence	Petal color	Petal width	Date, first flowers	Number of leaflets	Sepal length	Petal length	Akene color	Pubescence	Winter activity	Anthocyanin	Leaf length	Height	Akene weight			Index value
Column no. on card........	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	..
Data to be punched........	..	2	5	7	2	1	3	1	3	3	1	4	5	5	6	7	4	9	..	..	54

through the run. A further check was made after each sorting by seeing that the holes punched in the column selected for each group were aligned.

After the data were tabulated in the form shown in table 7, the correlation coefficient, *r*, between the pairs of characters was computed.

A third useful application of the punched card method is to select from among an entire population individuals that have specified combinations of characters. This has been done in the study of the F_2 population of Timberline × Oak

TABLE 7

Sample tabulation showing frequencies of F_2 plants of Upper Monarch Lake × Santa Barbara classified with respect to two characters

Length of leaves, classes	Degrees of winter activity at Stanford, classes						Totals
	Do_1*	Do_2	Do_3	Do_4	Do_5	Do_6	
Ll_1†	5	15	1	6	0	0	27
Ll_2	5	44	8	35	0	0	92
Ll_3	3	42	14	125	4	1	189
Ll_4	8	31	13	195	17	8	272
Ll_5	1	7	7	160	47	8	230
Ll_6	0	0	3	65	44	16	128
Ll_7	0	2	1	18	18	7	46
Ll_8	0	0	0	1	9	3	13
Totals	22	141	47	605	139	43	997

* Do_1, the most winter-dormant class at Stanford and comparable to the Upper Monarch Lake parent; Do_6, the most winter-active class and similar to the Santa Barbara parent; other values are intermediate.

† Ll_1, class with leaves 4 to 8 cm. long at Stanford; Ll_8, leaves 32 to 36 cm. long; intermediate classes represent 4-cm. intervals.

The correlation coefficient *r* for these two characters is +0.54, which, for the sample of 997 plants here tabulated, is highly significant.

Grove, for example, in which recombinations of the morphological and physiological characters occur, and where the effects of contrasting environments on these recombinations were observed. The machine-selected cards representing groups of plants meeting certain specifications were listed by means of a tabulating machine. Groups of F_2 plants thus selected were then compared in respect to their performance in contrasting environments. Chapter III is largely devoted to an analysis of such comparisons.

THE SEGREGATING HYBRID PROGENIES

Upper Monarch Lake × Santa Barbara. This cross between the alpine and the coastal races combines the most strikingly different ecological races from the central California transect.

The principal differences distinguishing the Upper Monarch Lake and the

Santa Barbara parental races and their F_1 hybrid are listed in table 8. The two reciprocal hybrids were identical as far as could be determined in the Stanford garden from a culture of 35 F_1 plants using Santa Barbara, and 6 F_1's using Upper Monarch Lake, as the female parent. In almost all characters the hybrids were clearly intermediate between the parents, as table 8 indicates, although

TABLE 8

CHARACTERS OF PARENTS AND F_1 HYBRIDS OF UPPER MONARCH LAKE × SANTA BARBARA AT STANFORD

Character	Ssp. *nevadensis,* Upper Monarch Lake, 1134-1	F_1 hybrids, 3299–3300	Ssp. *typica,* Santa Barbara, 1119-1
Climate of native habitat	alpine, continental	....	mild coastal
Rhizomes	many, long	some, short	none
Leaves, length	6–10 cm.	15–23 cm.	25–35 cm.
Leaves, width	1–2 cm.	3–6 cm.	8–12 cm.
Stems, length	10 cm.	55–65 cm.	50–60 cm.
Anthocyanin	none	red	purplish red
Pubescence	glabrescent	fairly glabrescent	densely villous
Glands	almost none	intermediate	abundant
Branching of inflorescence	almost erect	fairly erect	divaricate
Density of inflorescence	open	fairly dense	dense
Bracts subtending inflorescence	small, 3 leaflets	fairly large, 5 leaflets	large and leafy, 7 leaflets
Sepals, length	6 mm.	8 mm.	9–10 mm.
Receptacle	small, not fleshy	intermediate	large and fleshy
Petals, color	white	white	cream-white
Petals, length	6 mm.	7–8 mm.	3–4 mm.
Petals, width	6–7 mm.	6 mm.	3 mm.
Akenes, color	light buff	intermediate	dark brown
Akenes, weight	9 mg. per 100	19 mg. per 100	30 mg. per 100
Winter response	dormant	moderately active	strongly active
Date of first flowers	April 10	April 8	April 5
Self-compatibility	self-sterile	self-fertile	self-fertile

some characters, such as the large petals of the alpine parent, appeared as dominants in the F_1.

An outstanding feature of the F_1 was its marked hybrid vigor in the Stanford garden as compared with either parent. This enhanced vigor was in part expressed as taller stems, longer leaves, and larger flowers than would otherwise be anticipated on the basis of strict intermediacy. The parents and their hybrid are shown in figure 10.

Figure 11 shows photographs of samples of segregating F_2's from a uniform garden at Stanford. There are striking differences between the parents and

FIG. 10. Upper Monarch Lake (*left*) and Santa Barbara (*right*), and their F_1 hybrid (*center*).

Parents photographed from herbarium specimens taken from the garden at Stanford, and the F_1 from a living plant, all to the same scale; the black-and-white scale is 10 cm. high, the squares 1 cm.[2]

FIG. 11. Sample F_2 progeny from the cross Upper Monarch Lake × Santa Barbara in a uniform garden at Stanford. The plants were 2 years old when photographed, and all are to the same scale.

among the segregating F_2 plants in gross characters such as length of stems, mode of branching of inflorescences, and size of leaves. There are also many slighter differences in characters such as pubescence, color of petals, size and color of akenes, and degree of anthocyanin pigmentation that are not evident in the illustrations. Physiological characters, such as differences in time of flowering and in degree of winter activity, also segregate and are superimposed upon the morphological segregations.

A study of the reshuffling of an array of 14 pairs of characters in the F_2 provided the data for the present genetic analysis. The variability of these characters was so continuous that it was difficult to classify the F_2 individuals into distinct phenotypes. They were therefore rated according to a numerical scale representing degrees of expression. Those quantitative characters that could be measured, such as length of stems (height) and weight of akenes, were classified on this basis. Other characters, however, such as degree of anthocyanin coloration and degree of winter activity, were scored according to an arbitrary scale and accordingly are subject to the uncertainties of such a classification.

In table 9 are listed the class limits of the variations of each character among the F_2 of this cross, and also the frequencies of the individuals within each class. Classes that depend upon a subjective rating may show peculiarities in the frequency distribution of individuals. For example, under petal color, 685 individuals are listed in the table as being white, 207 as cream, and only 78 as intermediate. It is possible that only two classes for flower color should have been considered, reflecting an approximate segregation of 3 white to 1 cream, and that dominance is incomplete so that some of the heterozygotes appear as intermediates.

INDEX VALUES OF F_2'S OF THE CROSS UPPER MONARCH LAKE × SANTA BARBARA. In setting up the classes that describe the variations of each of the 14 characters, the lowest class values (class 1) were used to represent the alpine parent, and the highest to indicate the coastal parent.

By taking the sum of the class values of all the 14 characters listed in the table for any given plant, a number is obtained which is an approximate measure of a given plant's characteristics as indicated on a numerical scale ranging from one parental type to the other. The sum of the class values, here called the index value, is useful in making general comparisons. For example, the index value of the Upper Monarch Lake parent is 16, while that of the Santa Barbara parent is 67. The F_1 has an index value of 48, and plant 257 used as an example in table 6 has a value of 54, indicating that it resembles the Santa Barbara parent more closely than the Upper Monarch Lake.

The index values of the F_2 plants can be plotted as a frequency curve, as in figure 12. The variability within the F_2 population follows a moderately regular frequency curve with the intermediate classes having the highest frequencies. The irregular shape of the curve and the fact that the mean of the population falls below the index value of the F_1 suggest that the F_2 plants are produced through complicated gene recombination as far as the 14 characters listed in

table 9 are concerned. Neither of the parental types, however, was recovered in the F_2 as judged on the basis of these characters. This is not surprising because, on the basis of probability, the sample of 1015 F_2 plants grown is much too small to yield parental-type individuals even if only one gene were responsible for each of the 14 characters.

Scarcely any of the 14 characters studied rest on a simple Mendelian basis. Therefore, unless genetic linkage is present, millions of F_2 plants would be required before even a single plant of either parental type could reasonably be expected. If the numerous unlisted character differences between the parents were also to be taken into account, the possibility of recovering an exact match of either parent in an F_2 would become remote indeed. Fortunately, however, it is not necessary to recover the exact parental types in order to analyze the genetic systems that determine the differences between them if the F_2 is large enough to permit an analysis of the gene systems that govern individual characters.

SEGREGATION OF AKENE WEIGHT IN UPPER MONARCH LAKE × SANTA BARBARA. When segregations for individual characters rather than for combinations of 14 characters are studied, the problem of genetic analysis becomes simpler. By way of an example, the inheritance of akene or seed weight in the progeny of the hybrid Upper Monarch Lake × Santa Barbara may be considered. This quantitative character is of a kind that might be expected to be governed by a series of multiple genes.

Seed weights were determined on samples of 50 seeds per plant, and all the seeds were harvested on plants grown at Stanford. The mean akene weight of the Upper Monarch Lake parent was 8.8 mg. per 100; that of the coastal Santa Barbara parent was 30.2 mg. per 100 akenes, more than three times as much. The seed weight of the F_1 parent, 3299-3, was 19 mg. per 100 seeds, close to the mean of the parents, 19.5 mg. per 100. Other F_1 individuals of the same parentage, however, had weights as low as 15 or 16 mg. per 100.

The variability among the F_2 progeny ranged from a plant having a seed weight comparable to that of the alpine parent to 26 plants having a weight higher than the Santa Barbara parent. The curve in figure 13 shows the frequency distribution of the 961 F_2 plants to the various classes of seed weight. The seed weights of the parents and the F_1 are indicated along the scale at the bottom of the graph. The frequency curve can be compared with the data in table 9. It is evident that the mean seed weight of the F_2 plants is higher than that of the F_1, and that there is transgressive segregation toward heavier seeds.

If one proceeds from the hypothesis that the inheritance of seed weight in this cross is governed by a series of multiple genes, and that each gene of the series has an equal effect without dominance, then, by means of the binomial formula, the expected frequencies of the classes of phenotypes in an F_2 of the size of the present one can be calculated. Table 10 lists the expected frequencies under such conditions in a population of 961 individuals on the basis of the assumption that 1, 2, 3, 4, or 5 pairs of genes are responsible for the segregation.

TABLE 9

SEGREGATION OF CHARACTERS IN F_2 PROGENY OF UPPER MONARCH LAKE × SANTA BARBARA INTO VARIOUS CLASSES

Characters	Classes and frequencies										Totals
	1	2	3	4	5	6	7	8	9	10	
Inflorescence											
Classes	open	dense	.....	.....	.....	.....	.....	.....	.....	.....	
Frequencies	301	671	.....	.....	.....	.....	.....	.....	.....	.....	972
Petal color											
Classes	white ⟶		cream	.....	.....	.....	.....	.....	.....	.....	
Frequencies	685	78	207	.....	.....	.....	.....	.....	.....	.....	970
Petal width											
Classes	wide ⟶		narrow	.....	.....	.....	.....	.....	.....	.....	
Frequencies	494	88	388	.....	.....	.....	.....	.....	.....	.....	970
Date, first flowers											
Classes	March	April	May	.....	.....	.....	.....	.....	.....	.....	
Frequencies	243	650	79	.....	.....	.....	.....	.....	.....	.....	972
Bracts, leaflet number											
Classes	3	5	7	.....	.....	.....	.....	.....	.....	.....	
Frequencies	252	584	136	.....	.....	.....	.....	.....	.....	.....	972
Sepal length (mm.)											
Class limits	4–6	6–8	8–10	10–12	.....	.....	.....	.....	.....	.....	
Frequencies	68	678	223	3	.....	.....	.....	.....	.....	.....	972
Petal length (mm.)											
Class limits	11–9	9–7	7–5	5–3	.....	.....	.....	.....	.....	.....	
Frequencies	18	585	363	4	.....	.....	.....	.....	.....	.....	970

Akene color											
Classes	light →				dark	.....	.....	.....	.....	.....	
Frequencies	4	162	144	643	10	.....	.....	.....	.....	.....	963
Pubescence											
Classes	glabrate →		glandular pubescent			.....	.....	.....	.....	.....	
Frequencies	0	1	194	599	176	.....	.....	.....	.....	.....	970
Winter dormancy											
Classes	dormant →					active	.....	.....	.....	.....	
Frequencies	22	141	47	605	139	43	.....	.....	.....	.....	997
Anthocyanin											
Classes	green →					anthocyanous		.....	.....	.....	
Frequencies	36	90	83	72	132	527	56	.....	.....	.....	996
Leaf length (cm.)											
Class limits	4–8	8–12	12–16	16–20	20–24	24–28	28–32	32–36	.....	.....	
Frequencies	27	92	189	272	230	128	46	13	.....	.....	997
Height (cm.)											
Class limits	5–15	15–25	25–35	35–45	45–55	55–65	65–75	75–85	.....	.....	
Frequencies	15	54	120	222	292	166	85	17	.....	.....	971
Seed weight (mg. per 100)											
Class limits	7–10	10–13	13–16	16–19	19–22	22–25	25–28	28–31	31–34	34–37	
Frequencies	1	8	40	203	154	302	140	87	20	6	961

The number of 961 individuals also corresponds fairly closely to the number of individuals classified in the segregation of other characters of this cross.

When all genes have an equal additive effect, the frequency curve of the F_2 segregation should follow the binomial curve; it should be symmetrical, the

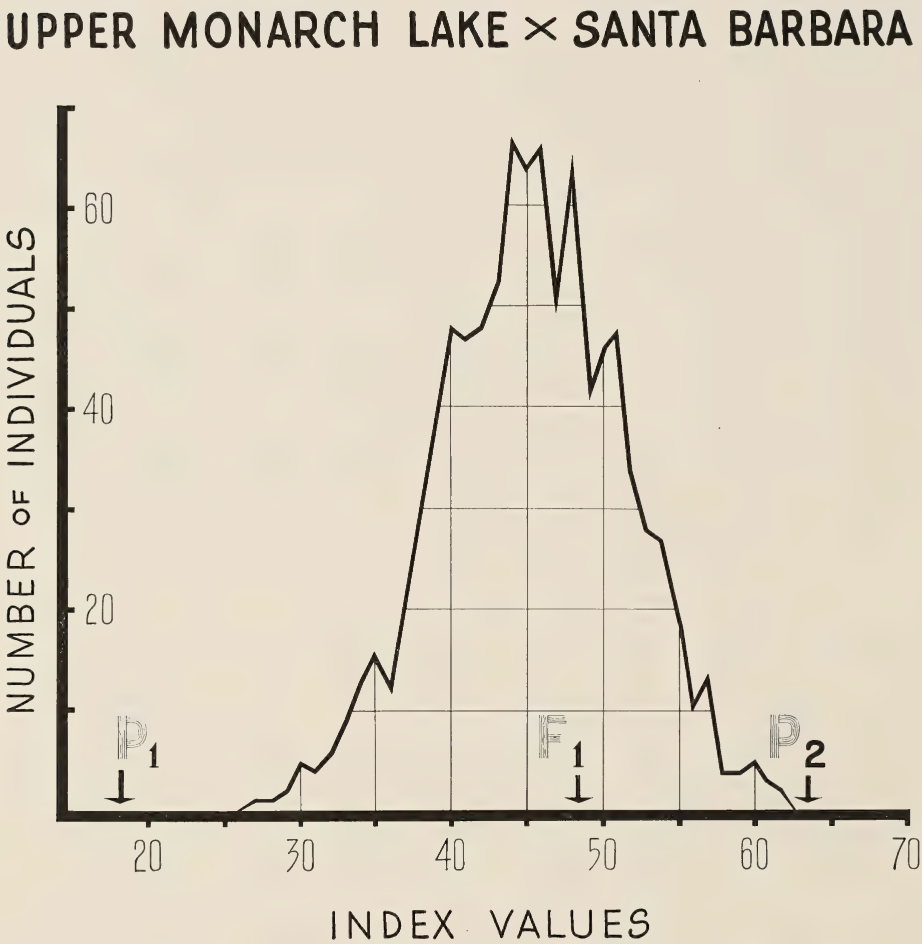

Fig. 12. Frequency diagram showing distribution of index values among 952 F_2 progeny of Upper Monarch Lake × Santa Barbara.

Index values are an approximate measure of degree of similarity to the parents and their F_1 hybrid. See text.

positions of the F_1 and of the mean of the F_2 should coincide, and there should be no transgression beyond the parental extremes.

The binomial segregation ratios in table 10 furthermore indicate that, when only one or two pairs of genes having equal additive effect segregate, the central and the extreme classes, which represent the F_1 and the parental types, contain all or a large percentage of the F_2 individuals. As the number of contributing

genes increases, however, the F_2 individuals segregate over a greater number of classes at the expense of the center and the two extreme groups, and become extremely difficult to distinguish. The phenotypic expressions of the genotypes may overlap so much that classification may become uncertain when as few as two pairs of genes are involved.

The best measure of the number of additive genes governing a character is the frequency of the parental types appearing in the F_2. Further aids in inter-

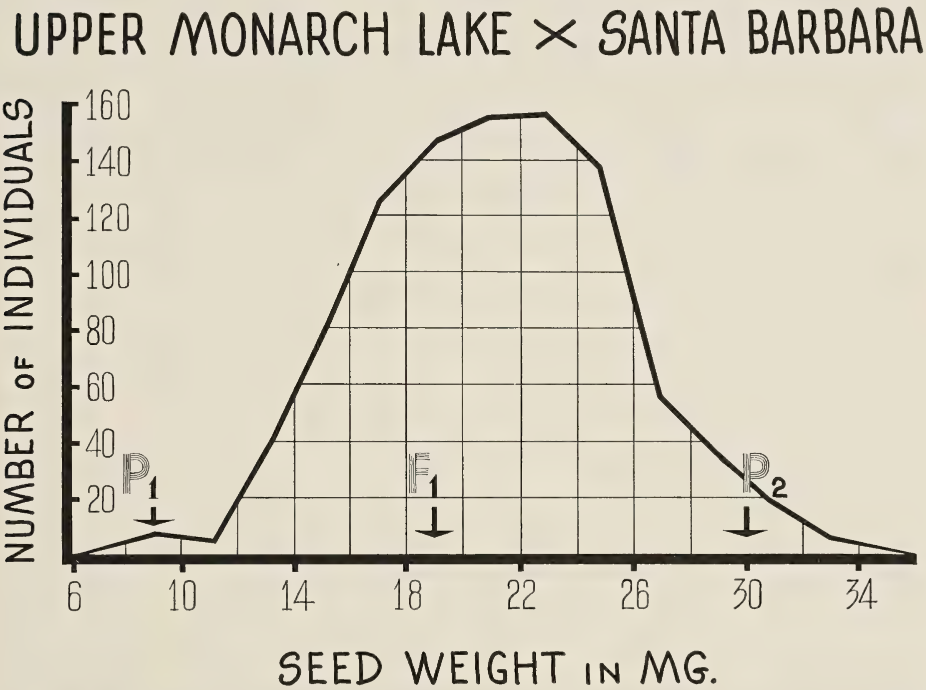

FIG. 13. Frequency diagram showing distribution of seed weight among 961 F_2 progeny of Upper Monarch Lake × Santa Barbara as compared with the parents and their F_1 hybrid.

pretation are provided by the shape of the frequency curve plotted against classes and by the position of the F_1 hybrid.

If dominance is involved for any of the genes, radical shifts from the theoretical class frequencies indicated in table 10 may occur. Likewise, if two pairs of genes governing the same character are genetically linked, the ratios will change as though fewer genes were operating. The frequencies of the various classes will also be strongly modified if several genes acting on one character have unequal value in influencing its expression; if one gene has an overwhelming effect, the segregation will approach a one-gene ratio, and the other genes will function as modifiers.

Another complication is the possible interplay between genes that influence the

expression of a character in opposite directions, as for example between some that may decrease weight and some that may increase it. Such a situation may cause transgressive segregation, so that the F_2 will segregate beyond the limits expressed by the parents.

Transgressive segregation can also result if the two parents contain complementary genes having effects that supplement each other when brought together. In all these situations, the ratios of the various classes in a segregating F_2 will be modified from the theoretical idealized binomial ratios indicated in table 10.

Returning to our example of seed weights in the F_2 of Upper Monarch Lake × Santa Barbara, it is obvious that the frequency curve in figure 13 deviates considerably from a theoretical binomial curve. The low frequency with which the alpine type was obtained in the F_2 would suggest that approximately five pairs of polymeric genes may govern seed weight. A much higher frequency of 87 plants fell in the same class as the coastal parent, and 26 F_2 plants even exceeded the seed weight of this parent. Such a transgressive segregation, associated with the general increase in mean seed weight in the F_2 above that of the F_1, could be produced by the interaction of genes of opposing effect. For example, the large-seeded coastal parent may possess an inhibitor for seed size that the alpine parent lacks, so that the small-seeded alpine parent might in part be responsible for the extra-large seeds appearing in some F_2 plants. The minimum number of genes that govern the segregation of seed weight in this cross is therefore probably about five pairs in addition to one pair of inhibitors.

TABLE 10

BINOMIAL DISTRIBUTION IN A POPULATION OF 961 INDIVIDUALS FOR A SERIES OF POLYMERIC GENES HAVING EQUAL EFFECTS

No. of pairs of genes	Ratios and expected frequencies
1	1 : 2 : 1 240.25 480.50 240.25
2	1 : 4 : 6 : 4 : 1 60.1 240.2 360.4 240.2 60.1
3	1 : 6 : 15 : 20 : 15 : 6 : 1 15.0 90.1 225.2 300.5 225.2 90.1 15.0
4	1 : 8 : 28 : 56 : 70 : 56 : 28 : 8 : 1 3.75 30.0 105.0 210.25 263.0 210.25 105.0 30.0 3.75
5	1 : 10 : 45 : 120 : 210 : 252 : 210 : 120 : 45 : 10 : 1 0.95 9.4 42.2 112.6 197.1 236.5 197.1 112.6 42.2 9.4 0.95

The evidence gained from a study of segregation ratios in the F_2 of the present hybrid, and of the F_2 and the F_3 populations of the next hybrid to be dis-

cussed, Timberline × Oak Grove, indicates that the inheritance of other characters of *Potentilla glandulosa* is generally determined by systems of genes similar to those that control seed weight. The analysis of the remaining 13 characters will therefore be deferred until after an introductory discussion of the second hybrid.

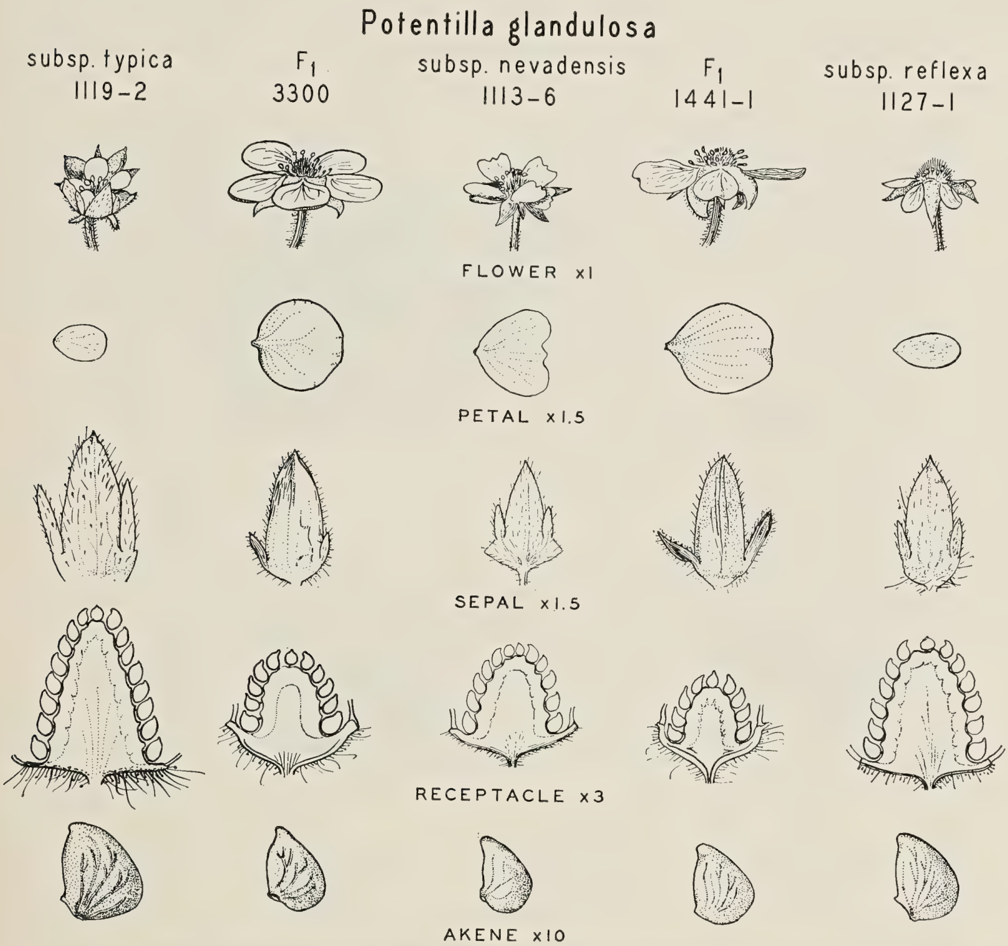

FIG. 14. Details of floral and fruit characters of parental plants and their F_1 hybrids. See tables 8 and 11.

TIMBERLINE × OAK GROVE. In many respects the hybrid Timberline × Oak Grove parallels Upper Monarch Lake × Santa Barbara, but it involves another taxonomic subspecies, and the characters segregating in the F_2 are also to some extent different.

One of the principal features of the genetic study of this cross was the testing of the cloned F_2 progeny in the three contrasting climates at the Stanford, Mather, and Timberline transplant stations. The results of this phase of study

will be reported in more detail in chapter III. In the present chapter we shall confine our attention to the more strictly genetic aspects as seen primarily at Stanford, although the observations at the mountain stations will necessarily enter to some extent in the interpretation of the expression of some of the characters.

Details of flower and fruit characters distinguishing the parents and F_1 are depicted in figure 14. The parents and their reciprocal F_1's as they appear when grown in the Stanford garden are shown in figure 15. All characters considered,

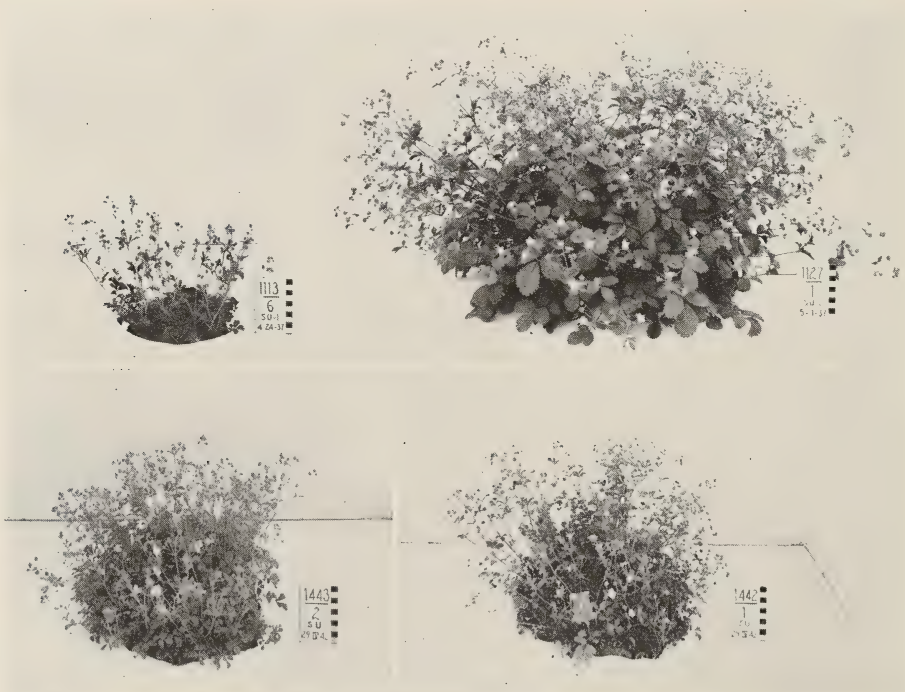

FIG. 15. Parents, Timberline (*upper left*) and Oak Grove (*upper right*), and their reciprocal F_1 progeny (shown below their respective maternal parents), all in the garden at Stanford. All plants shown to the same scale. See table 11.

the contrast between the parents is fully as great as that between the parents of Upper Monarch Lake × Santa Barbara. The F_1 plants of Timberline × Oak Grove and its reciprocal, like those of Upper Monarch Lake × Santa Barbara, show some hybrid vigor.

Table 11 lists the characters of the parents and F_1 of this cross in detail. This list includes both morphological and ecological characters, and also the responses of the parents and the F_1 at the mountain stations. A description of the parents and the F_1 with particular emphasis on their survival characteristics at the Stanford, Mather, and Timberline stations has previously been presented in Volume I of this series (Clausen, Keck, and Hiesey, 1940, pp. 114–123).

Like the F_2 of Upper Monarch Lake × Santa Barbara, the F_2 of Timberline × Oak Grove shows striking segregation as illustrated by the sample plants in figure 16. Only the more obvious character differences such as those between length of stems, size of leaves, mode of branching, and size of plant are visible in the picture, but segregation in petal size, shape, and color, in pubescence of leaves and stems, in degree of anthocyanin coloration, and in other, less conspicuous, characters is equally complete. The F_2 progeny were fertile and yielded widely segregating F_3 progenies that likewise recombined the characters of the original parents.

TABLE 11

CHARACTERS OF PARENTS AND F_1 HYBRIDS OF TIMBERLINE × OAK GROVE AT STANFORD

Character	Ssp. *nevadensis,* Timberline, 1113-6	F_1 hybrids, 1442-1 + 1443-2	Ssp. *reflexa,* Oak Grove, 1127-1
Native habitat	subalpine zone	....	warm, dry foothills of Sierra Nevada
Growth at transplant stations	weak at Stanford, vigorous at Mather and Timberline	vigorous at Stanford and Mather, strong at Timberline	vigorous at Stanford and Mather, dies at Timberline
Life form	hemicryptophyte, without woody crown	chamaephyte, with a short woody crown	chamaephyte, with a branching, woody crown
Rhizomes	many, long	few, short	none
Leaves, length	9–12 cm.	18–23 cm.	24–30 cm.
Leaves, width	3–4 cm.	4–5 cm.	5–7 cm.
Stems, length	13 cm.	35 cm.	45 cm.
Anthocyanin	none	moderately anthocyanous	deeply anthocyanous
Pubescence	lightly pubescent	moderately pubescent	strongly pubescent
Glands	few	moderately abundant	abundant
Habit of branching	almost erect, strict	intermediate	divaricate, flexuous
Petal color	white (ivory)	cream	deep yellow (lemon chrome)
Petal shape	cuneate, notched	oval, slightly notched	oblanceolate, entire
Petal size	medium (because of notch)	large	very small
Petal width	wide	wide	narrow
Petal orientation	upcurved	rotate to upcurved	reflexed
Akenes, color	light buff	intermediate	reddish brown
Akenes, size	small	intermediate	large
Self-compatibility	self-sterile	intermediate	self-fertile

Table 12 shows the range of the F_2 segregation into classes for 13 characters studied, the class limits for each character, and the number of individuals falling into each class. As in the previous cross, the more alpine characteristics were given the lowest class value, and those of the foothill parent the highest.

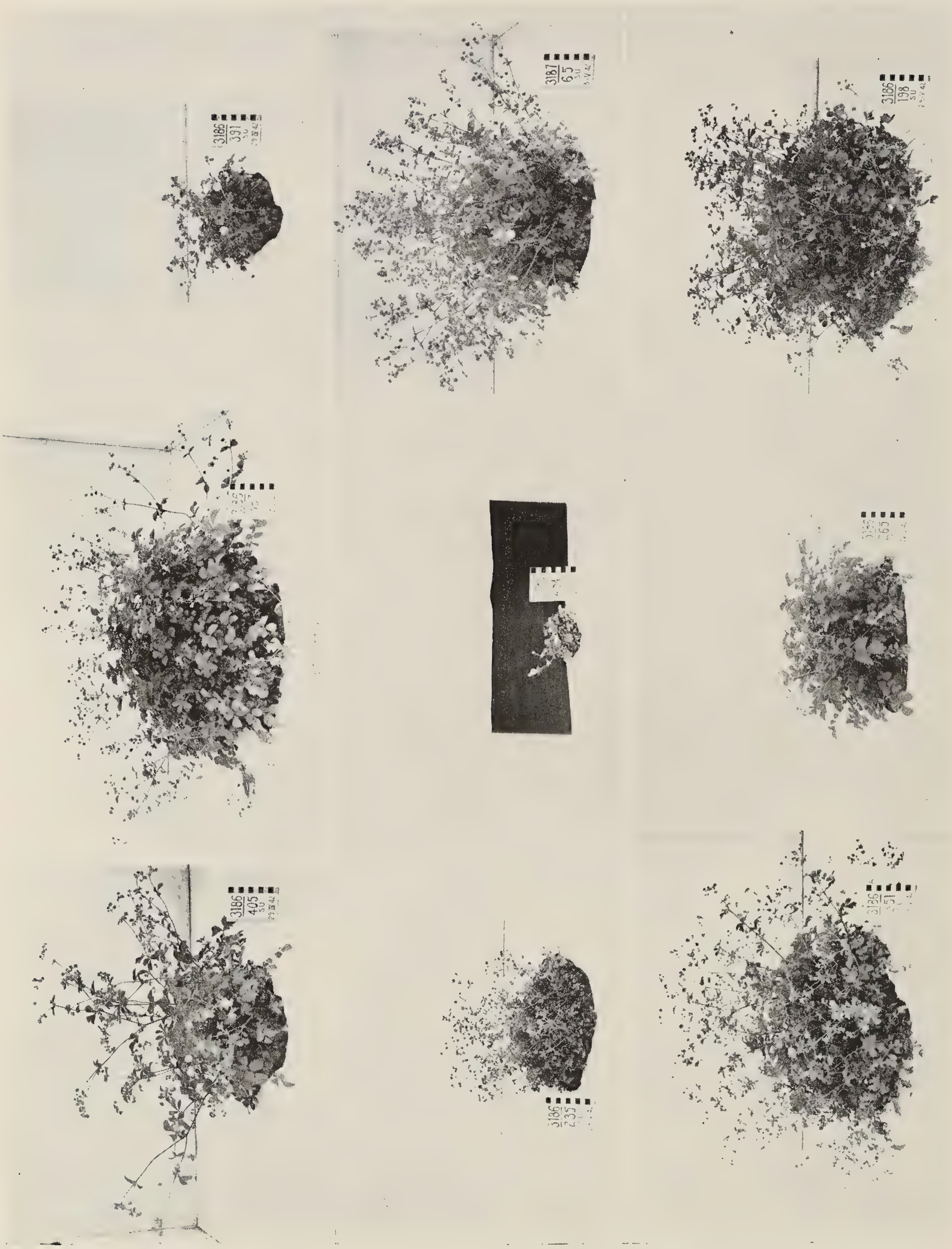

FIG. 16. Sample F_2 progeny of Timberline × Oak Grove in a uniform garden at Stanford. The 6-year-old plants were photographed to the same scale in spring 1942.

INDEX VALUES IN THE CROSS TIMBERLINE × OAK GROVE. The index value for 12 of the characters listed in table 12 was computed for each F_2 plant in the Timberline × Oak Grove cross by the method explained on page 38. The 12 characters are those listed in table 12, but do not include crown height because too many plants had died before dependable data on this character could be obtained. Data from Mather were used in computing the index values for leaf length, height of plant, and date of first flowers. Frost susceptibility was observed at Timberline only, whereas data from all stations were used in determining the survival pattern.

The index values, plotted as a frequency distribution curve in figure 17, provide a picture of the over-all range of variability in the F_2. All the F_2 individuals fall between the ranges of the parents, but none of the parental combinations were realized in the F_2.

Because transgressive segregation occurs in several characters, as, for example, time of flowering, the potentially possible lowest value with reference to the graph in figure 17 would be 12, and the potentially highest 62, transgressing the range between the index values of the two parents.

Although in relation to the potentially possible segregations this F_2 population is small, the 575 F_2 plants of the Timberline × Oak Grove hybrid apparently represent a fair sample of the genetic recombinations that can reasonably be expected in a cross between races from such distinct climates. When single characters are considered, this F_2 population serves as a fairly satisfactory sample for genetic analysis.

F_3 POPULATIONS OF THE CROSS TIMBERLINE × OAK GROVE. The study of the segregation of characters in the F_2 is strengthened by the data obtained from 20 F_3 progenies. Twenty F_2 plants were selected for self-pollination in screened garden cages to represent various recombinations of the parental characters for further genetic analysis. Table 13 lists the 20 parent F_2 plants, the F_3 cultures derived from them, and some of the characteristics of both the F_2 and F_3 plants. The seeds from the self-pollinated F_2's were in some instances collected both at Stanford and at Timberline. The seeds harvested from each station were grown separately at Stanford, and the progeny were compared in the same uniform environment. These parallel cultures are listed together in table 13.

The total number of plants in the 20 F_3 cultures was 2043. The progenies differed in the number of individuals as indicated by table 13. It is highly probable that the difference in the number of seeds obtained from the parental F_2 individuals resulted from differences in their degree of self-fertility, inasmuch as the alpine parent was self-incompatible and the foothill self-compatible.

One of the outstanding features of these F_3 progenies was the extent to which segregation continued to take place in them. These segregations indicated that more extensive genetic recombination was possible than was evident from the F_2 data.

TABLE 12

SEGREGATION OF CHARACTERS IN F_2 PROGENY OF TIMBERLINE × OAK GROVE INTO VARIOUS CLASSES

CHARACTER	CLASSES AND FREQUENCIES								TOTALS
	1	2	3	4	5	6	7	8	
Petal orientation									
Classes	± upcurved	reflexed	.....	.....	.....	.....	.....	.....	
Frequencies	550	26	.....	.....	.....	.....	.....	.....	576
Petal width									
Classes	± wide	narrow	.....	.....	.....	.....	.....	.....	
Frequencies	558	18	.....	.....	.....	.....	.....	.....	576
Petal notch									
Classes	notched →			→ entire	.....	.....	.....	.....	
Frequencies	93	254	57	171	.....	.....	.....	.....	575
Petal length									
Classes	long →				→ short	.....	.....	.....	
Frequencies	278	115	94	47	41	.....	.....	.....	575
Petal color									
Classes	white →				→ yellow	.....	.....	.....	
Frequencies	70	86	206	162	49	.....	.....	.....	573
Crown height (cm.)									
Class limits	0–2	3–8	9–13	.....	.....	.....	.....	.....	
Frequencies	31	306	97	.....	.....	.....	.....	.....	434
Branching									
Classes	erect →		→ divaricate	.....	.....	.....	.....	.....	
Frequencies	181	222	113	.....	.....	.....	.....	.....	516

Anthocyanin									
Classes	green	→	→	anthocyanous	.....	.....	.....	.....	
Frequencies	20	122	314	94	25	.....	.....	.....	575
Frost susceptibility									
Classes	resistant	→	→	susceptible	.....	.....	.....	.....	
Frequencies	84	168	112	79	80	.....	.....	.....	523
Leaf length (cm.)									
Class limits	4–8	8–12	12–16	16–20	20–24	24–28	28–32	32–36	
At Stanford, frequencies	53	155	187	98	26	0	1	0	520
At Mather, frequencies	8	33	72	127	128	92	57	6	523
Stem length (cm.)									
Class limits	1–10	10–20	20–30	30–40	40–50	50–60	60–70	.....	
At Stanford, frequencies	8	75	222	160	47	6	1	.....	519
At Mather, frequencies	5	35	109	173	135	48	14	.....	519
First flowers, dates									
At Stanford: Class limits	Mar. 21–28	Mar. 28–Apr. 3	Apr. 3–11	Apr. 11–18	Apr. 18–25	Apr. 25–May 2	May 2–9	May 9–16	
At Stanford: Frequencies	5	64	133	168	89	41	8	3	511
At Mather: Class limits	May 1–8	May 8–15	May 15–22	May 22–29	May 29–June 5	June 5–12	June 12–19	June 19–26	
At Mather: Frequencies	2	46	177	245	35	7	3	1	516
Survival pattern									
Periods of survival* At Stanford	short	short	short	short	long	long	long	long	
Periods of survival* At Mather	short	long	long	short	long	short	long	short	
Periods of survival* At Timberline	long	long	short	short	long	long	short	short	
Frequencies	26	56	68	58	148	25	97	64	542

* Short survival: plants died before end of experimental period.
Long survival: plants lived throughout experimental period.

One objective in obtaining the F_3 populations was to determine whether new, stabilized ecologic races could be recognized as beginning to emerge from such a hybrid population. Although the continued high segregation in the F_3's counteracted this aim, the most contrasting F_3 populations were nevertheless distinct from one another, as can be seen from the means listed in table 13. The F_3 offspring of the alpine-like plant -484 were very short-stemmed, those of -89

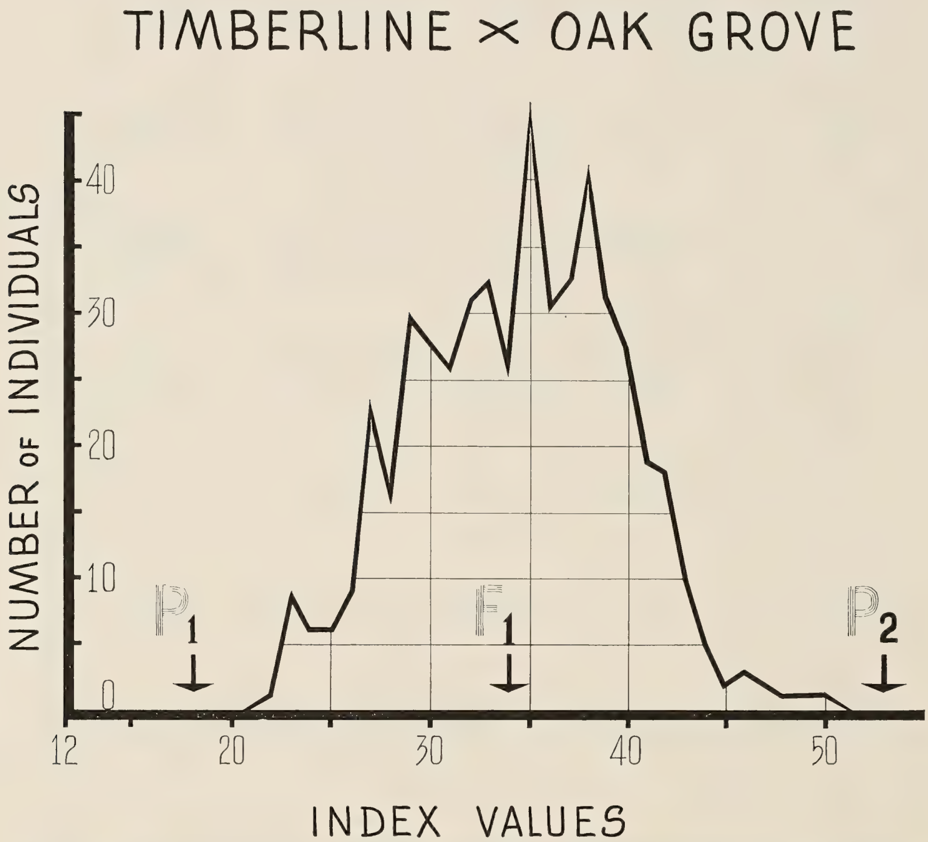

FIG. 17. Frequency diagram showing distribution of index values among 521 F_2 progeny of Timberline × Oak Grove.

Index values indicate a summation of character expressions among the progeny as compared with the parents and their F_1 hybrid.

fairly short-stemmed, and those of -405 long-stemmed. There was but little overlap among these three sets of progeny. In contrast with these, the offspring of plant -118 were intermediate in stem length and overlapped widely with other progenies.

It is clear that in the F_3 the progeny from the F_2 plants -484, -89, and -405 are already distinct enough to give rise to distinguishable lines. It can reasonably be concluded that, after several generations, races could be selected almost as distinct

TABLE 13

CHARACTERISTICS OF F_2 PLANTS OF TIMBERLINE × OAK GROVE AND THEIR PROGENY
(S=Stanford, M=Mather, T=Timberline)

F_2 plants				F_3 progeny grown at Stanford			
Plant no.	Vigor rating* at S–M–T	Stem height (cm.) at S–M–T	Index value†	Origin of seed	No. of individuals	Mean length of stems (cm.)	Mean width of rosette (cm.)
-5	4–5–3	25–37–26	27	S	22	26.4±1.9	30.9±2.3
-6	4–5–4	32–34–29	31	S	85	27.2±0.7	32.8±1.0
				T	31	28.9±1.7	33.7±1.6
-28	5–5–6	33–48–41	28	S	10	39.0±3.7	30.0±2.1
				T	11	32.3±2.0	28.7±2.8
-65	5–6–4	46–61–28	34	S	214	37.6±0.7	32.9±0.7
				T	9	32.8±3.3	27.2±3.7
-89	4–4–4	31–37–29	33	S	179	26.5±1.8	28.8±0.7
				T	2	30.0±4.1	61.0±4.5
-118	5–6–4	43–60–29	33	S	293	40.1±0.6	29.9±0.6
				T	11	35.9±4.2	27.7±3.0
-123	4–6–3	41–55–25	36	S	51	38.7±1.3	30.9±1.1
				T	8	37.5±4.5	31.3±3.2
-198	5–6–4	45–50–30	43	S	37	39.3±1.4	35.3±1.2
-235	4–5–3	30–38–20	32	S	16	26.9±2.6	20.6±2.0
-265	4–5–3	50–51–33	37	S	437	43.4±0.7	30.0±0.4
				T	26	41.9±2.4	30.4±2.1
-315	5–5–2	43–38–43	38	S	433	46.4±0.5	38.3±0.4
-351	6–6–2	52–40–33	45	S	356	41.7±0.5	39.5±0.5
-365	6–6–2	44–56–30	48	S	236	39.2±0.6	41.2±0.8
-387	6–6–2	52–50–20	39	S	342	42.6±0.6	37.3±0.5
-391	4–5–1	42–54–0	40	S	33	34.4±2.0	17.1±1.0
-405	5–5–2	53–52–30	43	S	317	49.7±0.7	36.1±0.5
-425	3–2–3	24–17–25	29	S	15	16.3±1.3	17.7±1.5
				T	15	17.7±1.5	25.0±2.3
-484	2–4–5	15–34–33	29	S	22	15.0±1.2	14.6±1.0
-473	3–3–3	29–36–28	28	S	44	21.8±1.5	17.3±1.3
-545	4–5–3	41–38–31	35	S	20	42.5±1.8	35.5±1.7

* 1 indicates lowest vigor, 6 the highest.
† Cf. figure 17.

as those represented by the original parents. In the more widely segregating F_3 progenies, selection would probably have to be practiced through more generations before comparable differences between selection products would be realized.

Genetic linkage would tend to counteract recombination, although after crossovers have occurred it also favors the selection of new ecotypes. Most of the heritable characters of *Potentilla glandulosa* are tied together by partial linkages that tend to favor the original parental combinations. This aspect is presented in some detail in later pages of this chapter.

A question of basic importance is whether differences in environment can affect selection either between gametes or in embryonic stages of seed development among F_2 plants. Seeds from ramets of the same individuals grown in the extreme environments of Stanford and Timberline were harvested separately, and the resulting progeny were grown under uniform conditions at Stanford. The number of F_3 seedlings obtained from the ramet at Timberline, however, was very small, because there the plants have fewer flowers and the short growing season and frequent frosts at the alpine station permit only part of the seed crop to mature. Such conditions might be presumed to favor some kind of natural selection in the gametic or embryonic stages of seed development.

The progenies grown from seed harvested at Timberline were too small to allow detection of statistically significant differences between them and those obtained from seed harvested on the same individual at Stanford. As examples of such differences, the data for length of stems and width of rosettes of progenies from seed harvested at the Stanford and Timberline stations are given in table 13.

GENIC ANALYSIS OF CHARACTERS

The data from the study of variation in natural races grown in a uniform environment, and the analysis of the inheritance of selected characters in the F_1, F_2, and F_3 progeny, furnish a basis for a fair estimate of the mode of inheritance of typical characters differentiating climatic races of *Potentilla glandulosa.* We shall therefore examine in detail the evidence on the inheritance of various segregating characters in the two crosses, Upper Monarch Lake × Santa Barbara, and Timberline × Oak Grove.

1. Orientation of Petals

The orientation of the petals, varying from upcurved to reflexed, is used as one of the key characters distinguishing the subspecies of *Potentilla glandulosa.* This character appears to be governed by a relatively simple system of genes. The genes for upcurved petals of subspecies *nevadensis* tend to mask partially the effect of the gene or genes for reflexed petals in subspecies *reflexa.* This tendency is evident even in the F_1 of the cross Timberline × Oak Grove, and is illustrated in figure 14.

The ratios observed in the segregating F_2 and F_3 populations suggest that a minimum of three pairs of genes are responsible for the inheritance of *upcurved*

as contrasted with *reflexed* petals. Of the 576 individuals in the F_2, 550 were classified as rotate or upcurved, and 26 as reflexed. As shown in table 14, this is close to a 61:3 ratio characteristic of a system determined by three pairs of genes, one pair of which acts in a direction opposite to that of the other two. Such a system requires two multiple epistatic genes which tend to make the petals erect or upcurved, E_1 and E_2, and one fairly hypostatic gene, R, which in the absence of the E genes makes the petals reflexed. Plants with at least one E gene, or plants recessive for both the E and the R genes ($e_1e_1e_2e_2rr$), will have upcurved to rotate petals, hence the ratio 61:3 instead of 60:4. Only plants with strictly reflexed petals were placed in the reflexed class. The group of plants classified as upcurved or rotate contained plants of various degrees of upcurvedness. The phenotypic expression of the genotype may fluctuate even between different flowers on one plant. For example, frequently a few flowers on an intermediate plant were slightly reflexed, although the majority of flowers had rotate or upcurved petals; such plants were classified as upcurved. The classification was based upon observations over a period of years on cloned divisions grown at the three transplant stations.

The F_3 progeny obtained from the selfing of phenotypically distinct F_2 individuals yielded various proportions of plants with fully reflexed petals, as is shown in table 14. Two F_3 progenies segregated in the proportion 15 upcurved to 1 reflexed, four according to the ratio 3:1, and three 13:3. All these progenies were derived from upcurved to rotate F_2's segregating reflexed progeny. One reflexed F_2 individual, -198, produced rotate-flowered plants, but it was impossible to separate the heterozygote Rr phenotype from the reflexed RR and the recessive and rotate rr types. Two F_2 plants with reflexed petals, -351 and -365, yielded essentially only reflexed progeny; a few rare exceptions with rotate petals in the two progenies probably represent phenotypic modifications of the reflexed genotype. Eight progenies of F_2 plants with upcurved petals were constant and

TABLE 14

INHERITANCE OF ORIENTATION OF PETALS IN F_2 AND F_3 PROGENY OF TIMBERLINE × OAK GROVE

Timberline, 1113-6 ———————— × ———————— Oak Grove, 1127-1
$E_1E_1E_2E_2rr$, upcurved* $e_1e_1e_2e_2RR$, reflexed*

F_1: $E_1e_1E_2e_2Rr$, rotate

F_2 SEGREGATION

PHENOTYPES	FREQUENCIES			GENOTYPES
	Observed	Calculated	Ratio	
upcurved to rotate	550	549.0	61	$E\cdots$ or $e_1e_1e_2e_2rr$
reflexed	26	27.0	3	$e_1e_1e_2e_2R$
Total	576	576.0	64	

(*Continued on following page*)

TABLE 14—*Continued*

F_3 SEGREGATION

F_2 PARENTS			F_3 PROGENIES, OBSERVED AND CALCULATED FREQUENCIES†			
Plant no.	Phenotypes	Suggested genotypes	Non-reflexed	Reflexed	Totals	Ratios
-5......	upcurved	EE····	17	....	17	
-6......	upcurved	EE····	117	....	117	
-28.....	upcurved	EE····	21	....	21	
-65.....	upcurved	EE····	223	....	223	
-89.....	upcurved	EE····	170	....	170	
-118....	upcurved to rotate	$E_1e_1E_2e_2RR$	263 281.3	37 18.7	300 300.0	15:1
-123....	upcurved	$E_1e_1e_2e_2RR$	45 47.5	17 15.5	62 62.0	3:1
-198....	reflexed, occasionally rotate	$e_1e_1e_2e_2Rr$	21 (rotate) 9.3	16 27.7	37 37.0	1:3
-235....	upcurved	$E_1e_1e_2e_2RR$	10 12.0	6 4.0	16 16.0	3:1
-265....	upcurved to rotate	$E_1e_1e_2e_2Rr$	368 367.4	83 84.6	451 451.0	13:3
-315....	rotate to slightly reflexed	$E_1e_1e_2e_2Rr$	355 349.3	75 80.7	430 430.0	13:3
-351....	reflexed	$e_1e_1e_2e_2RR$	3 0.0	346 349.0	349 349.0	
-365....	reflexed	$e_1e_1e_2e_2RR$	5 0.0	222 227.0	227 227.0	
-387....	rotate to slightly reflexed	$E_1e_1e_2e_2Rr$	290 278.7	53 64.3	343 343.0	13:3
-391....	rotate	EE··RR or eeeerr	33	....	33	
-405....	upcurved to rotate	$E_1e_1E_2e_2RR$	279 283.1	23 18.9	302 302.0	15:1
-425....	upcurved to rotate	$E_1e_1e_2e_2RR$	26 29.3	13 9.7	39 39.0	3:1
-473....	rotate to upcurved	EE····	39	....	39	
-484....	upcurved to rotate	$E_1e_1e_2e_2RR$	14 14.3	5 4.7	19 19.0	3:1
-545....	rotate	EE··RR or eeeerr	20	....	20	

* E_1 and E_2: multiple genes influencing the petals toward the erect position.
R: gene that in the absence of E ($e_1e_1e_2e_2$) reflexes the petals.
† Frequencies without decimal fractions are observed; those with decimals, calculated.

yielded F_3's with only upcurved petals. As is indicated in table 14, the parents of these F_3's were interpreted as having become homozygous for either the E_1 or the E_2 gene, or for both.

The observed frequencies of upcurved as compared with reflexed petals in the F_2's and the F_3's are very close to the calculated ratios. The F_2's were classified repeatedly and independently in different years and at different stations, so that there appears to be considerable assurance that the three-gene system here proposed is correct, or at least a close approximation of the true genetic basis of petal orientation in the two subspecies *nevadensis* and *reflexa*. Other subspecies of *Potentilla glandulosa* exist, however, that have more erect petals than *nevadensis*, and presumably other genes govern these differences.

2. Petal Notch

The subalpine parent used in the cross Timberline × Oak Grove had the peculiar trait of having the petals notched at the apex, as shown in figure 14. This character, which occurred as a spontaneous variant in the wild, was found in a natural population growing near the Timberline station. The plant displaying this character, 1113-6, was dug and used as a parent in crosses with lowland forms because of its promise as a distinguishing marker in genetic experiments. The character reappeared in many kinds of combinations in F_2 and F_3 progenies and provided conclusive evidence of the transfer of genes of the original subalpine parent to plants with greatly diverse characteristics.

Petal notch is unique among the characters studied because it occurred on a single individual as a spontaneous variant. From a taxonomic point of view it therefore has no significance, in contrast with the difference between reflexed and upcurved petals, which has long been used as a key character distinguishing subspecies *reflexa* from the others. Petal notch was originally supposed to have arisen through recent mutation, and it was anticipated that it would be governed by perhaps a single pair of genes. It is now clear that it is governed by at least three pairs of genes with the likelihood that there may be more.

In the F_1 progeny the notched character was barely expressed: the petals were mostly not notched, but occasionally a few flowers would show a slight dentation at the tip of the petals, especially on clones grown at the mountain stations. In the F_2 the segregation was not clear-cut. The plants were grouped into 4 classes as indicated in tables 12 and 15. On the basis of observations during a number of years at three stations on the 575 F_2 plants that were classified, 93 had fully notched petals at all three transplant stations, 254 were more or less notched, 57 were entire when grown at Stanford but more or less notched at Mather and Timberline, and 171 had entire petals at all three stations.

The results from the study of the segregating F_2 and F_3 progenies are summarized in tables 15 and 16. The ratios of the segregations in the various F_3 progenies may be accounted for on the assumption that at least three pairs of genes are involved, namely, one positive gene for notch, N, balanced against two

TABLE 15

THEORY OF INHERITANCE OF PETAL NOTCH IN TIMBERLINE × OAK GROVE

Timberline, 1113-6 ——————×—————— Oak Grove, 1127-1
$NNi_1i_1i_2i_2$, strongly notched $nnI_1I_1I_2I_2$, entire
F_1, 1442-1 and 1443-2: $NnI_1i_1I_2i_2$, partly notched

Genotypes			Phenotypes In F_2	Phenotypes In F_3 (Stanford only)
16 nn			16 entire	entire
32 Nn	8 I_1I_1	2 I_2I_2	2 entire	entire
		4 I_2i_2	4 trace	entire
		2 i_2i_2	2 ± notched	entire
	16 I_1i_1	4 I_2I_2	4 trace	entire
		8 I_2i_2	8 ± notched	entire
		4 i_2i_2	4 ± notched	± notched
	8 i_1i_1	2 I_2I_2	2 ± notched	entire
		4 I_2i_2	4 ± notched	± notched
		2 i_2i_2	2 notched	notched
16 NN	4 I_1I_1	1 I_2I_2	1 entire	entire
		2 I_2i_2	2 ± notched	entire
		1 i_2i_2	1 ± notched	entire
	8 I_1i_1	2 I_2I_2	2 ± notched	entire
		4 I_2i_2	4 notched	entire
		2 i_2i_2	2 notched	± notched
	4 i_1i_1	1 I_2I_2	1 ± notched	entire
		2 I_2i_2	2 notched	± notched
		1 i_2i_2	1 notched	notched
Total		64	64	....

F_2 SEGREGATION

Classes*	Frequencies Observed	Calculated	Ratio
4, entire	171	171.0	19
3, trace	57	72.0	8
2, ± notched	254	234.0	26
1, fully notched	93	99.0	11
Totals	575	575.0	64

N: gene for notched petals.
I_1 and I_2: multiple inhibitors for notched petals.
* Numbers of classes refer to those in table 12.

pairs of genes inhibiting notch, I_1 and I_2. Although in the absence of the inhibitors the gene for notch acts as a dominant, its effects tend to be covered in the presence of the fairly epistatic inhibiting genes. Such a balanced three-gene system would explain moderately well the frequency of the phenotypes observed in the F_2 and F_3 progenies, and also the fact that intermediate classes are modifiable in different environments, and in different years in the same environment.

In table 15 are indicated the proposed genetic formulas for the parents, the expected genotypes in the F_2, and the corresponding phenotypes in the F_2 and the F_3. The observations on the F_3's were made only at Stanford and only for one year.

The plants that are homozygous for the notch gene, NN, and possess no more than two of the four possible inhibitors, have, according to the hypothesis outlined above, notched petals, as do also plants that are heterozygous for notch, Nn, and lack inhibitors. Plants that are recessive for notch, nn, and possess all four inhibitors are assumed to have entire petals. Individuals that are homozygous for notch, NN, and have three dominant inhibitors are considered to be those with more or less notched petals at all three stations. There is also a class having entire petals at Stanford but more or less notched petals when transplanted to the mountain stations, and these are probably heterozygous for notch with three pairs of inhibitors. Tables 15 and 16 show that for the extreme and most easily determined classes the observed frequencies are in good agreement with the theoretical ratios based on this hypothesis.

Some of the partially notched biotypes are so modifiable that the expression of the notched character may vary from year to year in the same environment from entire to partially notched. In classifying the F_3 progenies at Stanford during a single year, therefore, some of the groupings may not be as accurate as those made in classifying the F_2 plants. Nevertheless, the observed data closely fit the theoretical Mendelian ratios as is shown in table 16. In the F_3 populations at Stanford the ratios suggest that even the presence of a single inhibitor for notch was sufficient to remove the plant from the fully notched class. For example, the F_2 plant -351 had entire petals, but the ratio in its F_3 progeny of 15 entire to 1 fully notched indicates that it was heterozygous for two dominant genes inhibiting notch, and homozygous for the notch gene. The fact that one notched F_2 plant, -473, segregated seemingly dominant non-notched plants and that 13:3 ratios occurred suggests the presence of a positive gene for notch in addition to the inhibitors. The total of the three 13:3 segregations included 996 plants with entire or nearly entire petals, and 229 fully notched. This is a close fit to the theoretical frequencies 994.1 to 229.9, and provides supporting evidence for our hypothesis.

There are some observations, however, that we cannot account for to our complete satisfaction. For example, the F_3 progeny of plant -89, a plant with slightly notched petals, contained almost as many plants with fully notched as with entire petals. Selfing would exclude a 1:1 ratio, and the only other possibility would be a 9:7 ratio, which would require the existence of a comple-

TABLE 16

SEGREGATIONS FOR PETAL NOTCH AT STANFORD IN F_3 PROGENIES OF TIMBERLINE × OAK GROVE

F_2 PARENTS			F_3 PROGENIES			
Plant no.	Phenotypes	Suggested genotypes	Entire	Slightly notched	Notched	Totals
			RATIO 15 : 1			
-351......	entire	$NNI_1i_1I_2i_2$	290	35	24	349
			327.2	..	21.8	349.0
			RATIO 13 : 3			
-265......	± notched	$NnI_1i_1i_2i_2$	364	..	87	451
			367.4	..	84.6	451.0
-315......	± notched	$NnI_1i_1i_2i_2$	281	67	82	430
			349.3	..	80.7	430.0
-387......	entire	$NnI_1i_1i_2i_2$	284	..	59	343
			278.7	..	64.3	343.0
			RATIO 3 : 1			
-65......	± notched	$NNI_1i_1i_2i_2$	167	23	33	223
			167.3	..	55.7	223.0
-118......	± notched	$NNI_1i_1i_2i_2$	193	30	77	300
			225.0	..	75.0	300.0
-198......	± notched	$NNI_1i_1i_2i_2$	27	..	10	37
			27.7	..	9.3	37.0
-484......	± notched	$NNI_1i_1i_2i_2$	12	..	7	19
			14.3	..	4.7	19.0
			RATIO 1 : 3			
-473......	notched	$Nni_1i_1i_2i_2$	10	..	29	39
			9.7	..	29.3	39.0
			RATIO 7 : 9			
-89.......	± notched	$NnKki_1i_1i_2i_2$	82	..	88	170
			74.6	..	95.4	170.0
			NONSEGREGATING			
-405......	strongly notched	$NNi_1i_1i_2i_2$	....	..	302	302
-391......	strongly notched	NN····	....	..	33	33
-123......	entire	nn···· or N·II··	62	..	...	62
-235......	entire	nn···· or N·II··	16	..	...	16
-365......	entire	nn···· or N·II··	227	..	...	227
-425......	entire	nn···· or N·II··	39	..	...	39

For explanation of gene symbols except K, see table 15; for K, see text. Frequencies without decimal fractions are observed; those with decimals, calculated.

mentary gene for notch, K, so that the petals do not become notched unless both the N and the K genes are present and the I genes absent. Another difficulty for our three-gene theory arises from the fact that the three F_2 plants yielding the 13:3 ratios in the F_3 differed slightly in phenotypes, as also did the four that produced 3:1 ratios. This situation, together with the fact that some of the F_3 progenies contained individuals of intermediate type, whereas others segregated into clear-cut classes of entire or notched, causes us to believe that genes other than the main three discussed are active although they probably have a minor effect. It is possible that the presence or absence of a gene K, complementary to the gene N, might produce some difference in the penetrance of notch in the presence of the inhibitors. On the whole, the agreement between the theoretical three-gene system and the observed segregation is fairly good, although the delicacy of the balance between the genes of opposite action suggests the presence of other influences that cannot be resolved on the basis of the data available.

There appears to be genetic linkage between at least one of the genes governing the orientation of petals and one of the genes controlling notch, because notched and upcurved petals are more frequently associated than would be expected by free recombination. The observed value of the correlation coefficient is +0.125. There is a high theoretical probability that the two characters would be partially correlated because each of these characters is governed by at least three pairs of genes, and *Potentilla glandulosa* has only seven pairs of chromosomes. The two characters are associated in the subalpine parent.

3. Petal Color

The two crossings of which F_2 or F_3 progenies were grown differed considerably in the number of genes controlling petal color, and they will therefore be discussed independently.

Upper Monarch Lake × Santa Barbara. In the cross Monarch Lake × Santa Barbara the white or ivory petals of Monarch Lake are contrasted with the cream-colored petals of Santa Barbara. The difference is one of the smallest that can be reliably discerned in the series of petal colors to be found in this species.

The F_1 hybrid had white petals much like those of the Monarch Lake parent. The F_2's were classified into two groups, white and cream, which were fairly easily distinguishable. Some plants, however, were described as "white plus" or "white minus," and others as "cream plus" or "cream minus," indicating some variability within each class. The F_2 plants were classified by using the flowers of the alpine parent and the F_1 as standards for white, and the flowers of the Santa Barbara parent as the standard for cream. The observed and calculated frequencies of the two phenotypes based on a 3:1 ratio of segregation, and the hypothetical genotypes of the parents and the F_1, are listed in table 17. The genetic formulas shown in the table for the parents and the F_1 are developed on the basis of the more complex segregation in the F_2 and the F_3's of the cross Timberline × Oak Grove discussed below.

The hypothesis developed to account for the inheritance of petal color in *Potentilla glandulosa* assumes that Y genes cause the petals to be yellow, and that W genes tend to change yellow to cream or white. The phenotypic expression depends upon the balance between the number of dominant Y or W genes that the plant possesses.

The segregation in the present cross is assumed to depend upon only one pair of the W genes, W_2w_2, which in the presence of W_1W_1 whiten the lemon yellow of Y_2Y_2 from cream to white. The evidence for a one-gene ratio seems to be clear. The present segregation is between adjacent steps in petal color, and the apparent simplicity of inheritance in this cross is in contrast with the complexity of the inheritance of petal color in the next.

TABLE 17

INHERITANCE OF PETAL COLOR IN F_2 PROGENY OF UPPER MONARCH LAKE × SANTA BARBARA

Upper Monarch Lake, 1134-1 ——— × ——— Santa Barbara, 1119-1
$W_1W_1W_2W_2y_1y_1Y_2Y_2$, white — $W_1W_1w_2w_2y_1y_1Y_2Y_2$, cream
F_1, 3259-3: $W_1W_1W_2w_2y_1y_1Y_2Y_2$, white

F_2 classification	Observed	Calculated, 3 : 1 ratio
White, W_2	729	727.5
Cream, w_2w_2	241	242.5
Totals	970	970.0

W: genes for white petals. Y: genes for yellow.

Timberline × Oak Grove. Approximately five pairs of genes appear to determine the differences between the white petals of the subalpine Timberline plant of subspecies *nevadensis* and the deep yellow, nonbleaching petals of the Oak Grove foothill parent belonging to subspecies *reflexa.* The F_1 of the cross between these two parents has cream-colored petals similar to those of the Santa Barbara form of subspecies *typica.*

An especially striking segregation occurred in the F_2, ranging from plants that had whiter petals than the ivory of the Timberline and Monarch Lake plants to others that were as deep yellow as Oak Grove. It was also evident that lighter shades of yellow were present, but it was not until the segregation among the progeny of F_3 populations had been analyzed that clear evidence was obtained that at least three shades of yellow occurred, for some of the F_2 plants yielded progeny segregating lemon yellow, and in a few F_3 cultures an even paler form of yellow appeared occasionally.

The petal colors of the F_2 plants were classified into five groups according to color, as follows:

White (wh): Petals as white as or whiter than in the Timberline parent.
Cream-white (cr-wh): Less white than the Timberline parent, but not as colored as the F_1.

Cream (cr): Intermediate in color between the parents, like the F_1.
Cream-yellow (cr-y): More yellow than the F_1, halfway between the F_1 and the Oak Grove parent.
Deep yellow (y): As yellow as the Oak Grove parent.
Light yellow (lemon): Lighter yellow than Oak Grove, but not pale.
Pale yellow (pale): Very light or martius yellow.

The last three classes were originally all listed as yellow. When the two lighter and rare variants were recognized in the F_3 progenies, the 49 yellow plants in the F_2 were re-evaluated in terms of three grades of yellow. In computing the general linkage values of petal color with respect to other characters, however, all three classes of yellow were treated as one class.

Any one of the various petal colors listed above can exist in either a bleached or a nonbleached form, depending upon the presence or absence of a dominant gene for bleaching, B. The action of the bleaching gene is most obvious in the deep yellow phenotype, although cream-yellow may bleach to cream, and cream may bleach to cream-white or even to white. The presence of the bleaching gene, manifest through the difference between the color of flowers that have newly opened and the distinctly paler shade of older flowers, complicates the classification.

Modification in petal color at the transplant stations is another source of difficulty. The white and deep yellow plants remain white and deep yellow, respectively, at all three transplant stations, but some of the intermediate colors tend to become modified in the direction of white at higher altitudes, especially at Timberline.

The segregated classes of phenotypes and the observed ratios are best explained through the assumption that petal color is the result of the interaction of at least two pairs of multiple whitening genes, W_1 and W_2, and two pairs of genes for yellow: deep yellow, Y_1, and lemon yellow, Y_2. The interplay between genes for white color and those for the various steps of yellow is best visualized through the list of phenotypes and assumed genotypes of flower color in the parents, the F_1, and the F_2, as indicated in table 18.

The Timberline parent is considered to be homozygous for the genes for lemon yellow, for two pairs of whitening genes, and for the bleaching gene, the last three tending to cover the effect of lemon yellow. The Oak Grove parent, on the other hand, is assumed to be homozygous for the gene for deep yellow, but recessive for all whitening and bleaching genes. The F_1, being heterozygous for all five pairs of genes, is cream. Forms occur in the F_2 which are recessive for both the deep yellow and lemon yellow, $y_1y_1y_2y_2$, but which have the whitening and the bleaching genes, $W_1W_1W_2W_2BB$, and therefore appear to be whiter than the Timberline parent. Also, there are some that have obtained the Y_2 gene but not the Y_1 gene for deep yellow and none of the whitening genes. Such plants are lemon yellow instead of deep yellow as in the Oak Grove parent. Finally, plants occur that are recessive for all the yellowing and whitening genes, $w_1w_1w_2w_2y_1y_1y_2y_2$, and therefore are pale or martius yellow, the most recessive

TABLE 18

THEORY OF INHERITANCE OF FLOWER COLOR IN F_2 PROGENY OF TIMBERLINE × OAK GROVE

Timberline, 1113-6 ———————— × ———————— Oak Grove, 1127-1
$W_1W_1W_2W_2y_1y_1Y_2Y_2BB$, white ———— $w_1w_1w_2w_2Y_1Y_1y_2y_2bb$, deep yellow

F_1, 1442-1 and 1443-2: $W_1w_1W_2w_2Y_1y_1Y_2y_2Bb$, cream

FREQUENCIES IN F_2

Genotypes			Phenotypes
16 $W_1W_1W_2W_2$	4 Y_1Y_1	1 Y_2Y_2	6 cream
		2 Y_2y_2	
		1 y_2y_2	
	8 Y_1y_1	2 Y_2Y_2	
		4 Y_2y_2	6 cream-white
		2 y_2y_2	
	4 y_1y_1	1 Y_2Y_2	4 white
		2 Y_2y_2	
		1 y_2y_2	
64 WWWw	16 Y_1Y_1	4 Y_2Y_2	12 cream-yellow
		8 Y_2y_2	
		4 y_2y_2	28 cream
	32 Y_1y_1	8 Y_2Y_2	
		16 Y_2y_2	
		8 y_2y_2	12 cream-white
	16 y_1y_1	4 Y_2Y_2	
		8 Y_2y_2	12 white
		4 y_2y_2	
96 WWww	24 Y_1Y_1	6 Y_2Y_2	18 cream-yellow
		12 Y_2y_2	
		6 y_2y_2	6 cream
	48 Y_1y_1	12 Y_2Y_2	12 cream-yellow
		24 Y_2y_2	42 cream
		12 y_2y_2	
	24 y_1y_1	6 Y_2Y_2	
		12 Y_2y_2	12 cream-white
		6 y_2y_2	6 white

Genotypes			Phenotypes
64 Wwww	16 Y_1Y_1	4 Y_2Y_2	4 deep yellow
		8 Y_2y_2	36 cream-yellow
		4 y_2y_2	
	32 Y_1y_1	8 Y_2Y_2	
		16 Y_2y_2	
		8 y_2y_2	8 cream
	16 y_1y_1	4 Y_2Y_2	4 cream-yellow
		8 Y_2y_2	8 cream
		4 y_2y_2	4 white
16 $w_1w_1w_2w_2$	4 Y_1Y_1	1 Y_2Y_2	12 deep yellow
		2 Y_2y_2	
		1 y_2y_2	
	8 Y_1y_1	2 Y_2Y_2	
		4 Y_2y_2	
		2 y_2y_2	
	4 y_1y_1	1 Y_2Y_2	3 lemon yellow
		2 Y_2y_2	
		1 y_2y_2	1 pale yellow
Total		256	256

SUMMARY OF EXPECTED PHENOTYPES

Classes	Ratios
1. White	26
2. Cream-white	30
3. Cream	98
4. Cream-yellow	82
5. Deep yellow	16
Lemon yellow	3
Pale yellow	1
Total	256

W_1, W_2: multiple whitening genes; W_1 slightly the stronger.
Y_1: gene for deep yellow, epistatic over Y_2, lemon yellow.
$y_1y_1y_2y_2$: pale yellow (martius yellow).
B: bleaching gene for Y_1 and Y_2.

for petal color so far encountered. The interplay among such genes can account for the observed transgressive segregation in petal color. The action of the W genes tends to cover the effects of the Y genes, and, in turn, the deep yellow Y_1 tends to cover the paler lemon yellow Y_2, although there is not complete epistasis. This system would establish a delicate balance in the intermediate forms which could become modified somewhat in different environments, and may also be influenced by the bleaching gene, B.

Table 19 lists the genotypes and the observed and calculated frequencies of phenotypes in the F_2, and also the frequencies in the F_3 progenies. Through this means our theory can be tested. The observed frequencies are not always in close agreement with the calculated, but allowance needs to be made for the difficulties inherent in classification. The calculated ratios, moreover, are based on assumed free recombination and do not take into consideration the possibility of genetic linkage and crossover in the F_2's, which would shift the ratios.

The data presented in table 19 indicate that white and cream-white F_2 individuals produce no yellow F_3's and, conversely, that yellow F_2's do not produce white or cream-white F_3 progeny. The cream-yellow F_2's yield offspring varying around cream-yellow as a mean with few or no whites, but many yellows. On the other hand, the mean F_2 group, cream, tends to segregate the entire range from one extreme to the other like the F_1, but the cream phenotype can cover many genotypes. These observations, in addition to the segregation of several degrees of whites, creams, and yellows, suggest that at least two pairs of genes are responsible for the whitening influence and two for the yellowing influence. Probably some of these genes are also linked, because some progenies have a surplus of whites and others of yellows.

It is possible that other genes with modifying effect are at work besides the five pairs postulated, and that they are responsible for some of the deviations from the calculated ratios. Data from fourth and fifth generations would be required, however, to test this assumption.

4. Petal Width

The various forms of the alpine and subalpine subspecies *nevadensis* have wide petals in contrast with the narrower petals of both the coastal *typica* and the foothill *reflexa*. The petals of the Oak Grove form of *reflexa* were narrower than in most forms of this subspecies. The F_1's both of Upper Monarch Lake × Santa Barbara and of Timberline × Oak Grove have petals as wide as or wider than those of the high-altitude parent. The analysis of the segregations in the F_2's and F_3's of these crosses confirms the impression that the genes for wide petals in the high-altitude subspecies are dominant or epistatic over the genes for narrower petals in the lowland forms. The segregations indicate, however, that petal width probably is determined by a fairly complex system of genes.

Upper Monarch Lake × Santa Barbara. The inheritance of petal shape ap-

TABLE 19

INHERITANCE OF PETAL COLOR IN TIMBERLINE × OAK GROVE

Parents: Plant no.	Parents: Phenotypes and genotypes		Progeny, phenotypes and frequencies: White	Cream-white	Cream	Cream-yellow	Deep yellow	Lemon yellow	Pale yellow	Totals
			F_2 population from selfed F_1's							
	cream									
1442-1	$W_1w_1W_2w_2Y_1y_1Y_2y_2Bb$	Obs.	70	86	206	162	29	18	2	573
1443-2	Same	Calc.	58.2	67.7	219.6	182.7	35.9	6.7	2.2	573
		Ratio	26 :	30 :	98 :	82 :	16 :	3 :	1	256
			F_3 populations from selfed F_2's							
	white									
3186-391	$W_1W_1W_2W_2y_1y_1y_2y_2BB$	Obs.	33	...	....	....	....	...	..	33
3187-5	$W_1w_1W_2W_2y_1y_1Y_2y_2 \cdot\cdot$	Obs.	14	2	0	....	....	...	..	16
		Calc.	11.0	4.0	1.0	....	....	...	..	16
		Ratio	11 :	4 :	1	....	....	...	..	16
3186-28	$W_1w_1W_2W_2y_1y_1Y_2y_2 \cdot\cdot$	Obs.	10	←6→		5	....	...	..	21
		Calc.	14.4	←6 6→		0	....	...	..	21
		Ratio	11 :	4 :	1	....	....	...	..	16
	cream-white									
3187-6	$W_1W_1W_2w_2Y_1y_1y_2y_2BB$	Obs.	13	←104→		....	....	...	..	117
		Calc.	29.3	←87.7→		....	....	...	..	117
		Ratio	4 :	6 :	6	....	....	...	..	16
3187-65	$W_1W_1W_2w_2Y_1y_1Y_2y_2BB$	Obs.	60	←133→		30	....	...	..	223
		Calc.	38.3	←146.4→		38.3	....	...	..	223
		Ratio	11 :	14 :	28 :	11	....	...	..	64
3186-235	$W_1W_1W_2w_2Y_1y_1Y_2y_2 \cdot\cdot$	Obs.	1	6	5	4	....	...	..	16
		Calc.	2.7	3.5	7.0	2.8	....	...	..	16
		Ratio	11 :	14 :	28 :	11	....	...	..	64
	cream									
3186-118	$W_1w_1W_2w_2Y_1y_1Y_2y_2Bb$	Obs.	5	29	125	44	←97→			300
		Calc.	30.5	35.1	114.5	95.9	←22 2→			300
		Ratio	26 :	30 :	98 :	82 :	16 :	3 :	1	256
3186-123	$W_1w_1W_2W_2Y_1y_1Y_2y_2 \cdot\cdot ?$	Obs.	2	2	31	5	←22→			62
		Calc.	6.5	7.5	23.5	19.5	←5 0→			62
		Ratio	26 :	30 :	98 :	82 :	16 :	3 :	1	256

3186-265	$W_1w_1W_2w_2Y_1y_1Y_2y_2$ ··?	Obs.	12	57	230	80	←70→		2	451
		Calc.	45.7	52.8	172.8	144.5	←33.4→		1.8	451
		Ratio	26 :	30 :	98 :	82 :	16 :	3 :	1	256
	cream-yellow									
3187-89	$w_1w_1W_2w_2Y_1y_1Y_2y_2$ ··	Obs.	...	...	64	49	28	29	..	170
		Calc.	8.0	5.3	42.5	66.3	37.2	8.0	2.7	170
		Ratio	3 :	2 :	15 :	25 :	14 :	3 :	1	64
3186-198	$w_1w_1W_2w_2y_1y_1Y_2Y_2bb$	Obs.	...	...	....	19	....	18	..	37
		Calc.	...	...	9.3	18.4	....	9.3	..	37
		Ratio	...	...	1 :	2	.... :	1	..	4
3186-315	$W_1w_1w_2w_2Y_1Y_1Y_2y_2Bb$	Obs.	1	28	88	135	186	...	..	430
		Calc.	...	26.9	80.7	161.2	161.2	...	..	430
		Ratio	...	1 :	3 :	6 :	6	...	..	16
3186-365	$w_1w_1W_2w_2Y_1Y_1Y_2Y_2bb$	Obs.	...	...	61	119	47	...	..	227
		Calc.	...	...	56.7	113.6	56.7	...	..	227
		Ratio	...	...	1 :	2 :	1	...	..	4
3186-387	$w_1w_1W_2w_2Y_1y_1Y_2Y_2Bb$?	Obs.	...	...	39	61	241	2	..	343
		Calc.	...	...	21.4	193.0	107.2	21.4	..	343
		Ratio	...	...	1 :	9 :	5 :	1	..	16
3186-405	$W_1w_1w_2w_2Y_1Y_1Y_2y_2Bb$	Obs.	...	16	33	125	128	...	..	302
		Calc.	...	18.9	56.7	113.2	113.2	...	..	302
		Ratio	...	1 :	3 :	6 :	6	...	..	16
3187-425	$W_1W_1W_2w_2Y_1Y_1y_2y_2Bb$? alpine type	Obs.	...	...	....	15	24	...	..	39
		Calc.	...	...	9.7	19.7	9.7	...	..	39
		Ratio	...	...	1 :	2 :	1	...	..	4
	deep yellow									
3186-351	$w_1w_1w_2w_2Y_1y_1y_2y_2BB$	Obs.	...	...	....	....	246	...	103	349
		Calc.	...	...	....	....	261.7	...	87.3	349
		Ratio	...	...	....	....	3	...	1	4
3186-545	$w_1w_1W_2w_2Y_1Y_1Y_2Y_2$ ··	Obs.	...	...	1	1	18	...	..	20
		Calc.	...	...	....	5.0	15.0	...	..	20
		Ratio	...	...	....	1 :	3	...	..	4

See table 18 for explanation of gene symbols.
The segregations for the B gene are not considered in the present calculations.

pears to be least complicated in the cross Upper Monarch Lake × Santa Barbara, where an approximation of a 9:7 ratio was obtained, as is shown in table 20. In this F_2 a small class of intermediates was tabulated which were on the borderline between the parents.

The ratio of 9 having wide petals, like *nevadensis,* to 7 having narrowly obovate petals, as in *typica,* would suggest the complementary action of a gene, C, activating another gene, Wi, for wide petals. If the information from only this cross had been available, the genetic control of width of petals would have been assumed to be simple.

Timberline × Oak Grove. The Oak Grove *reflexa* parent has narrow petals that are linear-lanceolate and about 3 mm. wide. They are narrower than those

TABLE 20

INHERITANCE OF PETAL WIDTH IN UPPER MONARCH LAKE × SANTA BARBARA

Upper Monarch Lake, 1134-1 ——— × ——— Santa Barbara, 1119-1
WiWiCC, wide — wiwicc, fairly narrow

F_1, 3259-1: WiwiCc, wide

F_2 CLASSIFICATION

Phenotypes	Frequencies			Genotypes
	Observed	Calculated	Ratio	
wide	494 } 582	545.6	9	Wi·C·
intermediate	88 }			
narrow	388	424.4	7	wiwi·· or Wi·cc
Total	970	970.0	16	

The Wi gene is the Wi_3 of table 22; in terms of tables 21 and 22, both parents are $wi_1wi_1wi_2wi_2 \cdot\cdot Wi_4Wi_4nana$, accounting for the fact that the petals of Santa Barbara were wider than those of Oak Grove. The C gene is the same as in table 22.

of the Santa Barbara form of subspecies *typica.* The width of the petals in the subalpine parent, 1113-6, is somewhat reduced by the notch character, which also shortens the petal; consequently, the F_1's of Timberline × Oak Grove have wider petals than either parent.

The two reciprocal F_1 individuals that were used to produce the F_2's were phenotypically almost indistinguishable with regard to petal width. Nevertheless, the F_2 progeny originating from the F_1 plant 1443-2 (culture 3187, having Timberline as the maternal parent) yielded many more plants that were as narrow-petaled as Oak Grove than did progeny of the reciprocal 1442-1 (culture 3186). Superficially the frequency in culture 3187 would correspond to 1 narrow-petaled plant among 15 with broader petals, whereas in culture 3186 the ratio was approximately 1:255.

Table 21 summarizes the data concerning the inheritance of petal width as shown by F_2 and F_3 progenies of Timberline × Oak Grove, and indicates the

TABLE 21

Inheritance of petal width in Timberline × Oak Grove

Timberline, 1113-6 —— × —— Oak Grove, 1127-1

$Wi_1wi_1Wi_2wi_2Wi_3Wi_3c_3c_3Wi_4Wi_4nana$, petals wide — $wi_1wi_1wi_2wi_2wi_3wi_3C_3C_3wi_4wi_4NaNa$, petals narrow

F_1, 1442-1: $Wi_1wi_1Wi_2wi_2Wi_3wi_3C_3c_3Wi_4wi_4Nana = 3186$ in F_2

1443-2: $wi_1wi_1wi_2wi_2Wi_3wi_3C_3c_3Wi_4wi_4Nana = 3187$ in F_2

F_2 classification

Culture no.		± Wide	Narrow	Totals	Ratios
3186	Obs.	413	2	415	
	Calc.	412.9	2.1	415.0	4075 : 21
3187	Obs.	145	16	161	
	Calc.	147.5	13.5	161.0	235 : 21

F_3 segregations

F_2 parents			F_3 progeny, frequencies				
Plant no.	Phenotypes	Suggested genotypes		± Wide	Narrow	Totals	Ratios
3186-28	wide	$Wi_1wi_1wi_2wi_2wi_3wi_3 \cdot\cdot wi_4wi_4NaNa$	Obs.	18	3	21	
			Calc.	15.7	5.3	21.0	3 : 1
3186-118	wide	$wi_1wi_1wi_2wi_2wi_3wi_3 \cdot\cdot Wi_4wi_4Nana$	Obs.	240	60	300	
			Calc.	243.9	56.1	300.0	13 : 3
3186-123	wide	$wi_1wi_1wi_2wi_2Wi_3wi_3Ccwi_4wi_4NaNa$	Obs.	33	29	62	
			Calc.	34.9	27.1	62.0	9 : 7
3186-484	wide	$wi_1wi_1wi_2wi_2Wi_3wi_3CCwi_4wi_4NaNa$	Obs.	15	4	19	
			Calc.	14.7	4.3	19.0	3 : 1
3187-65	wide	$wi_1wi_1wi_2wi_2Wi_3wi_3CCwi_4wi_4NaNa$	Obs.	166	57	223	
			Calc.	167.3	55.7	223.0	3 : 1
3187-89	wide	$wi_1wi_1wi_2wi_2Wi_3wi_3CcWi_4wi_4Nana$	Obs.	152	18	170	
			Calc.	156.1	13.9	170.0	235 : 21
3187-425	narrow	$wi_1wi_1wi_2wi_2Wi_3wi_3ccwi_4wi_4Nana$?	Obs.	2	37	39	
			Calc.	9.7	29.3	39.0	1 : 3

(*Continued on following page*)

TABLE 21—*Continued*

NONSEGREGATING F_3'S FROM F_2'S HAVING WIDE PETALS

(Genotypes: $Wi_1Wi_1\cdot\cdot$, $\cdot Wi_2Wi_2\cdot\cdot$, $\cdot\cdot Wi_3Wi_3CC\cdot\cdot$, or $\cdot\cdot\cdot Wi_4Wi_4\cdot\cdot$)

F_2 parents	No. of F_3 individuals	F_2 parents	No. of F_3 individuals
3186-198	37	3186-391	33
3186-235	16	3186-405	301
3186-265	451	3186-473	39
3186-315	430	3186-545	20
3186-351	349	3187-5	17
3186-365	227	3187-6	117
3186-367	343		

For explanation of gene symbols see table 22.

assumed genotypes. It should be remembered that the plants classified as having narrow petals in this cross belong to a distinctly different class from the narrow-petaled plants in the cross Upper Monarch Lake × Santa Barbara, which have narrowly obovate petals. In the cross Timberline × Oak Grove the plants with narrowly obovate petals were classified as being wide.

Six F_3 progenies from both the F_2 cultures of Timberline × Oak Grove, all from wide-petaled F_2 plants, segregated plants with petals as narrow as those of Oak Grove. The narrow-petaled plants appeared in ratios approximating 3:1, 13:3, 9:7, and 15:1. One narrow-petaled F_2 plant, 3187-425, produced a small progeny of 37 plants having narrow linear-lanceolate petals, and 2 plants having narrowly obovate petals 4 mm. wide. Thirteen wide-petaled plants, however, did not segregate any F_3 plants with narrow, linear-lanceolate petals. Six of these progenies were large enough to have produced the narrow-petaled biotype even though it had occurred as rarely as in culture 3186.

Although the observed ratios fall fairly close to recognized ratios of segregation, some difficulty arises when it is attempted to fit these ratios to gene formulas. In order to account for all the observed segregation ratios in the F_2's and the F_3's, the interaction of about six pairs of diversified genes must be assumed. The infrequency of individuals with narrow petals in one of the F_2's suggests the presence of four pairs of multiple genes, Wi_1 to Wi_4, which independently act to widen the petals. The 9:7 ratio implies the presence of genes of complementary effect, and the 13:3 ratio observed in one large progeny suggests the action of genes of opposite effect.

In order to account for the observations as simply as possible, an activating gene, C, may be assumed, complementary to one of the four genes determining wide petals, for example Wi_3. Likewise may be assumed a gene, Na, that narrows the petals to the linear-lanceolate shape found in the Oak Grove parent, but that is hypostatic under all the Wi genes and cannot express itself in their

presence. Finally, it must be assumed that the biotype recessive for the Na and the four Wi genes has narrowly oval petals, as in subspecies *typica*.

In accordance with this hypothesis the Timberline parent, 1113-6, was heterozygous for two pairs of widening genes, Wi_1 and Wi_2. One of the F_1 parents, 1442-1, was apparently heterozygous for all six pairs of genes, for it yielded only 2 F_2 offspring with narrow petals among a population of 415. The other F_1 parent, 1443-2, was heterozygous for only four pairs of genes and yielded 16 F_2 progeny with narrow petals among a total of 161.

The interplay among the six pairs of genes active in the segregation of 1442-1, and the frequencies of the resulting genotypes and phenotypes, are shown in table 22. According to the hypothesis presented above, the supposed segregation 255:1 in the F_2 culture 3186 is governed by a six-gene system yielding progeny in the ratio 4075:21. The agreement with expectation is close. Likewise, the ratios in the F_2 culture 3187, and in the F_3 progeny of 3187-89, became 235:21 instead of 15:1.

It is with some reluctance that this fairly complex theory of the inheritance of petal width is proposed, but simpler hypotheses are inadequate. The present theory accounts for the various ratios for petal width observed in two F_2's and in the F_3 progenies. The presence of four epistatic and independent genes governing petal width, the homozygosity of any one of which is sufficient to prevent segregation of narrow petals, explains the high frequency of constant, wide-petaled progenies among the F_3. The hypothesis applies to the segregation observed in the cross Upper Monarch Lake × Santa Barbara as well. Complementary and inhibitory actions are to be expected in characteristics that are determined by physiological and biochemical processes, and petal width might well be determined by such processes.

It is possible that data from later generations would necessitate changes in the genotypes assigned to the various parental, F_1, and F_2 individuals. It is more likely, however, that such changes would be in the direction of a larger number of proposed genes than fewer. Nevertheless, an analysis like the present offers a glimpse of the dynamic genetic systems that underlie the variation observed within every natural population.

5. Petal Length

Length of petals is determined by a system of genes that appears to be as intricate as the system that determines their width, but the data on petal length are not so well documented.

Upper Monarch Lake × Santa Barbara. The long-petaled alpine race when crossed with the short-petaled coastal race yielded F_1 progeny in both reciprocals having petals almost as long as those of the alpine parent. In the F_2 the segregation ranged from plants with petals longer than those of the alpine parent to others as short as the Santa Barbara parent, and included all classes of intermediates.

Measurements on petal lengths were made on flowers in the same stage of development in the garden at Stanford in order to eliminate as far as possible the effect of modifications due to differences in degree of development, and to environment. Grouping the F_2 plants into classes of 1-mm. intervals yielded seven classes. In the computations for linkage studies, class intervals of 2 mm. were used. The F_2 frequencies at class intervals of 1 mm., and the position of the parents and the F_1, are shown in table 23.

Only 4 among the 970 F_2 plants had petals as short as the Santa Barbara parent, and 3 had extra-long petals between 9 and 10 mm. These low frequen-

TABLE 22

Theory of inheritance of petal width in Timberline × Oak Grove

F_1, 1442-1: $Wi_1wi_1Wi_2wi_2Wi_3wi_3C_3c_3Wi_4wi_4Nana$

F_2 ratios

Genotypes						Phenotypes
3072 Wi_1						3072 wide
1024 wi_1wi_1	768 Wi_2					768 wide
	256 wi_2wi_2	192 Wi_3	144 C_3			144 wide
			48 c_3c_3	36 Wi_4		36 wide
				12 wi_4wi_4	9 Na	9 narrow
					3 nana	3 ± wide
		64 wi_3wi_3		48 Wi_4		48 wide
				16 wi_4wi_4	12 Na	12 narrow
					4 nana	4 ± wide
Total						4096
Ratio						4075 wide : 21 narrow

Wi_1, Wi_2, Wi_3, Wi_4: essentially dominant, multiple genes for wide petals, epistatic over Na; any single Wi gene may produce wide petals.

C_3: complementary gene activating Wi_3.

Na: narrowing gene, changing narrowly obovate to linear-lanceolate; hypostatic under Wi_1, Wi_2, Wi_3C_3, and Wi_4.

Completely recessive: narrowly obovate; classified as wide.

cies in the extreme classes might suggest that about four pairs of genes determine the expression of this character. However, other data indicate that the inheritance is not so simple. For example, the F_1 is not intermediate between the two parents, but has petals almost as long as those of the alpine parent, a fact that suggests partial dominance of long petals. This interpretation, however, is in conflict with the fact that in the F_2 the frequency distribution among classes is asymmetrical, with shorter petals prevalent. Moreover, plants with longer petals than those of the alpine parent are segregated. A theory assuming that four pairs of genes with equal effect are responsible for the inheritance of petal length is therefore inadequate.

It is possible that the observed segregations result from the interaction of

dominant genes for long petals and inhibiting genes decreasing the petal size. A more detailed analysis of the variation within the parental strains, in the F_1, and also of generations later than the F_2 would be required before a reasonably satisfactory understanding of the inheritance of petal length in this cross might be expected.

Timberline × *Oak Grove*. In the cross Timberline × Oak Grove the inheritance of petal length was studied by relating this character to sepal length rather than by actual measurement. In the Timberline parent the petals exceed the length of the sepals, whereas in Oak Grove they are shorter than the sepals (figure 14). In the F_1 the petals were longer than the sepals, and, because of the partial suppression of the notched character described in pages 45 and 47, they were even longer than in the Timberline parent.

Complete segregation for petal length occurred in the second generation. After the extent of environmental modification in this character when observed

TABLE 23

SEGREGATION OF PETAL LENGTH IN F_2 PROGENY OF UPPER MONARCH LAKE (P_1) × SANTA BARBARA (P_2)

LENGTH OF PETALS	CLASS INTERVALS (MM.)							TOTAL
	3	4	5	6	7	8	9	10	
Frequencies	4	81	282	396	189	15	3		970
Position of parents....	P_2				F_1	P_1			

at the Stanford, Mather, and Timberline transplant stations had been taken into account, the F_2 plants were grouped into five classes as shown in table 24.

Clearly, long petals are dominant over short, but the segregation is more complex than would be expected if only a single pair of genes were involved. Short petals can also be dominant. A high frequency of 41 individuals having short petals was obtained in a second generation consisting of less than 600 individuals, but some of these seemingly recessive short-petaled F_2's segregated third-generation plants with fairly long petals. This finding indicates that, in addition to positive genes for long petals, there are also relatively dominant inhibiting genes.

The range of segregation for petal length in third-generation hybrids is compared with that in their F_2 parents in table 25. Some F_2 parents and progenies classified as having petals longer than the sepals are actually only intermediate in absolute length of petals, because their sepals are short; examples include the progenies of the F_2 plants -5, -391, and -473.

Most F_2 plants classified as having petals longer than the sepals segregated F_3's that covered the entire range from very short to very long petals; exceptions were -6, -28, and -65, which did not segregate F_3 plants with short petals, and two with only intermediate F_3 progeny, namely -198 and -545.

F_2's with intermediate petals can segregate progeny with short petals, and those with short petals can segregate intermediate petals, as table 25 shows. Long-petaled F_2 plants may segregate either the entire range or only intermediate types. On the other hand, certain long-petaled, intermediate, and short-petaled types may yield relatively constant progeny.

It is therefore evident that with respect to petal length genes are present that act in opposite directions, and, furthermore, that they can be masked by genes for long petals. It is not possible from the present data to arrive at a satisfactory estimate of the number of genes determining petal length in Timberline × Oak Grove, although apparently there are not less than three pairs, and possibly not more than four or five.

TABLE 24

SEGREGATION OF PETAL LENGTH IN F_2 PROGENY OF TIMBERLINE × OAK GROVE

Class and description	Frequencies
1. Petals longer than sepals in all environments	278
2. Petals varying on the same plant from slightly longer than sepals to equaling sepals	115
3. Petals intermediate, equaling sepals	94
4. Petals varying from same length as sepals to shorter than sepals	47
5. Petals shorter than sepals in all environments	41
Total	575

6. Sepal Length

The inheritance of sepal length was studied only in the cross Upper Monarch Lake (short sepals) × Santa Barbara (long sepals). Like petal length, sepal length appears to be controlled by a multigene system. Because the sepals increase in size as the fruit develops, the measurement of sepal length is subject to considerable error unless all plants are measured at the same stage of development. In the present study the longest sepal on each F_2 individual was measured in flowers at anthesis, and classes were set up at intervals of 1 mm.

The Monarch Lake parent has sepals only 6.5 mm. long, whereas those of Santa Barbara are 13 mm. in length. The F_1 average was 8.5 mm., 1.25 mm. short of the arithmetic mean between the parents.

The sepals of the 972 plants of the second generation ranged between 4.5 and 12.5 mm. The shortest were therefore shorter than those of the alpine parent, but the longest were scarcely as long as those of the coastal parent, as is further evident in table 26, which lists the classes. The median class of the F_2 is about 2 mm. below the mean of the parents, and on either side of this large central class the frequencies are asymmetrically distributed. As a consequence, individuals approaching the Coast Range parent in sepal length are very rare.

These facts suggest the action of either one pair of rather dominant inhibiting

TABLE 25

INHERITANCE OF PETAL LENGTH IN F_3 PROGENY OF TIMBERLINE × OAK GROVE

PETAL LENGTH IN RELATION TO SEPALS

F_2 parents			F_3 progeny, class frequencies			
Plant no.	Class	Description	Long	Intermediate	Short	Totals
-5	1	long	17 (6–8 mm.)	...	...	17
-473	1	long	39 (6–8 mm.)	...	...	39
-6	1	long	113 (8–9 mm.)	4 (7 mm.)	...	117
-28	1	long: 6 mm.	11 (8–9 mm.)	10 (5–7 mm.)	...	21
-65	1	long: 8 mm.	151 (8–10 mm.)	72 (6–7 mm.)	...	223
-235	1	long: 7 mm.	9 (8 mm.)	7 (4–6 mm.)	...	16
-89	1	long: 6 mm.	127 (8–9 mm.)	← 43 (4–7 mm.) →		170
-118	1	long: 6 mm.	151 (8–10 mm.)	← 149 (4–7 mm.) →		300
-123	1	long: 7 mm.	27 (8 mm.)	← 35 (5–7 mm.) →		62
-265	1	long: 8 mm.	299 (8–10 mm.)	← 152 (4–7 mm.) →		451
-391	2	intermediate to long	33 (6 mm.)	...	...	33
-315	1	longer than sepals	...	147 (6–7 mm.)	283 (4–5 mm.)	430
-365	2	intermediate: 4.5 mm.	...	51 (6 mm.)	176 (4–5 mm.)	227
-387	2	intermediate: 5 mm.	...	87 (6 mm.)	256 (3–5 mm.)	343
-484	2	intermediate to long	...	6 (5–6 mm.)	13 (3–4 mm.)	19
-198	3	intermediate: 4.5 mm.	...	37 (4–5 mm.)	...	37
-545	3	intermediate: 5 mm.	...	20 (5–5.5 mm.)	...	20
-351	4	intermediate to short: 4 mm.	...	7 (6–7 mm.)	342 (3.5–5 mm.)	349
-405	5	short: 3 mm.	...	1 (6 mm.)	301 (4–5 mm.)	302
-425	5	short	...	...	39 (4–5 mm.)	39

genes, or two pairs of inhibitors each with a complementary effect, counterbalanced by a group of about three or four pairs of multiple genes tending to increase sepal length.

TABLE 26

SEGREGATION OF SEPAL LENGTH IN F_2 PROGENY OF UPPER MONARCH LAKE (P_1) × SANTA BARBARA (P_2)

	Class intervals (mm.)										Total
	4	5	6	7	8	9	10	12	13	14	
Observed frequencies	10	58	258	420	191	32	2	1	..		972
Position of parents.......			P_1		F_1				P_2		

7. Akene Weight

The inheritance of akene weight was discussed at the beginning of the present chapter, pages 39 to 45. In the cross Upper Monarch Lake × Santa Barbara the seed weights of the parents were approximately 9 and 30 mg. per 100 seeds, respectively. Probably a minimum of five pairs of genes of the multiple type tending to increase seed weight are balanced against one pair of weight-decreasing genes in determining the observed segregation.

8. Akene Color

The inheritance of seed-coat color was studied only in one of the hybrids, namely, Upper Monarch Lake × Santa Barbara. The mature seeds of the high-altitude subspecies *nevadensis* are light buff, and those of the coastal subspecies *typica* dark brown.

The first-generation hybrid was approximately intermediate, and the F_2 segregated a range of shades including both of the parental extremes and all classes of intermediates. The pigment is not evenly distributed on the seed coats, but is laid in a pattern simulating the venation of leaves. As far as could be ascertained, none of the F_2's were lighter in color than the alpine parent, nor were any darker than the coastal parent.

The F_2 progeny were classified by comparing the colors of their mature seeds directly with those of the parents and the F_1. Five groups were recognized: plants with seed coats matching the alpine parent were classed as light buff (class 1), those matching the coastal parent as dark brown (class 5), and those matching the F_1 as intermediate (class 3). Plants with seed coats ranging in color between the alpine parent and the F_1 were placed in class 2, and those between the F_1 and dark brown, in class 4.

The observed frequencies of the five classes of seed-coat color are listed in table 27. The F_2 distribution is not symmetrical, class 4 being by far the largest. Class 3 may have been restricted in relation to the others because only plants

matching the color of the F_1 were included in this group, but such restriction would not affect the symmetry of the distribution. It is obvious that the majority of the second-generation plants belong to the darker brown fractions.

The fairly intermediate character of the F_1, and the segregation into many grades of color in the F_2, indicate that several pairs of genes with similar effects determine the inheritance of akene color. The rarity of the extreme parental types and the absence of transgressive segregation suggest that approximately four pairs of genes of the multiple type may be responsible, although the effects of the genes are probably not of the same order of magnitude.

In the cross Timberline × Oak Grove, the subalpine parent had the small, light buff seeds characteristic of subspecies *nevadensis,* and the Oak Grove foothill parent, belonging to subspecies *reflexa,* had reddish brown, fairly large seeds,

TABLE 27

Segregation of seed-coat color in F_2 progeny of Upper Monarch Lake × Santa Barbara

Class and description	Frequencies
1. Light buff (like alpine parent)	4
2. Between light buff and intermediate	162
3. Intermediate (like F_1 hybrid)	144
4. Between intermediate and dark brown	643
5. Dark brown (like coastal parent)	10
Total	963

a color less extreme than the dark brown of subspecies *typica.* The color of the first-generation hybrid was fairly intermediate, and there was segregation in the F_2 and the F_3 generations, but no detailed studies of these were undertaken.

9. Branching of the Inflorescence

An important characteristic that distinguishes the alpine subspecies *nevadensis* from the Sierran foothill subspecies *reflexa* is the mode of branching of the inflorescence. These differences can be observed in figure 15 on page 46. Data bearing on the inheritance of this character have been furnished in the cross Timberline (having erect branches) × Oak Grove (having divaricate branches).

Both reciprocal F_1 progeny were intermediate between the two parents in this character. Within a population of 516 F_2 plants, 181 were classified as "erect," 222 as "intermediate," and 113 as "divaricate," as is shown in table 12.

The classification regarding branching type was based on herbarium specimens of plants grown at Mather, where these habit differences came to expression best. None of the three classes was homogeneous, for all contained a range of variation. Within the group classified as "erect" were a number of individuals similar to the alpine parental type; and within the group classed as

"divaricate," some plants were similar to the Oak Grove parent. Although accurate classification of this highly variable character could not be made, the grouping into the three classes serves as a useful method for studying the general mode of inheritance of this character and its correlation with other characters.

This study can be followed another step by observing the general segregation among F_3 progeny of F_2 plants having phenotypically different kinds of branching. Seven divaricate F_2 plants yielded only divaricate F_3's, but three yielded segregating progeny. Two F_2 plants with erect branching yielded segregating progeny. Two F_2 plants with erect branching yielded only erect F_3 progeny, whereas others segregated, and five F_2's classified as intermediate segregated the entire range of variation including both parental types.

From the available evidence it appears that branching habit is genetically fairly simple, because nonsegregating progenies are frequent. Probably only one or two pairs of genes govern this character, although a more complex interaction of genes of oppositional effect is suggested by the observation that divaricates can segregate erects, and erects likewise can segregate divaricates.

Individuals with erect branches tend to have short stems; plants with divaricate branches, long stems. In the F_2, the positive correlation coefficient of 0.417 found between branching habit and length of stems on plants at the Mather transplant station probably indicates a strong genetic linkage. Correlation between these two characters was also readily evident in F_3 populations, a topic that will be discussed in more detail in later pages.

10. Density of Inflorescence

Density of inflorescence is determined by the relative length of the branchlets and pedicels, in contrast with the inflorescence habit, discussed above, which is governed by the angle between the side branches and the main stem axis. The alpine form, subspecies *nevadensis,* has relatively long floral branches in relation to the whole stem, whereas the coastal subspecies *typica* has shorter branches. Studies on the inheritance of this character have been limited to the cross Upper Monarch Lake (having "open" inflorescence) × Santa Barbara (with "dense" inflorescence).

The F_1 was fairly congested, and segregation in the F_2 ranged from extremely dense to plants having inflorescences as open as in any of the forms of *nevadensis.* Among 972 F_2 progeny, 301 were classified as "open" and 671 as "dense" (table 9), indicating that "dense" is dominant.

Although these figures suggest a 3:1 ratio, it is not likely that the inheritance of this character is governed by a single gene, because each of the two classes contained a considerable range of variation. An exact classification of plants is impossible on the basis of this rather indefinite character, for the grouping depends to a certain extent upon subjective judgment.

In the F_2 population about 3 per cent of the individuals carried a combination

of characters in which dense inflorescences, short, erect stems, large rosette leaves, large sepals, a large fruiting receptacle, and densely pubescent herbage were associated. Plant 257 illustrated in figure 11, upper row, extreme right, is an example. This combination is unlike either parent, and was conspicuous as a distinctive type in the gardens at Stanford. Although plants of this kind showed appreciable recombination of characters among themselves, there was a correlation in the principal architectural features. A significant correlation exists between density of inflorescence and length of leaves, number of leaflets, density of pubescence, and weight and color of akenes, as is shown in later pages.

11. Crown Height

One of the most distinctive differences between subspecies *nevadensis* from high altitudes and subspecies *reflexa* from the foothills is the architecture at and below the ground line. Subspecies *reflexa* is a rosette chamaephyte; that is, it develops a robust, fairly erect, branched, woody crown ending in large rosettes of leaves that die during the winter but remain as remnants protecting dormant buds until the following spring. Each year the woody crown increases a little in height, pushing its rosettes of leaves upward. The crown of an 8-year-old plant of the Oak Grove parent grown at Mather extended 27 cm. above the ground. Below ground level the foothill form develops a branched, fairly vertical, robust tap root which more or less corresponds to the equally branched, fairly erect palmetto-like tussock above the ground.

Plants of alpine and subalpine *nevadensis,* on the other hand, are rhizome hemicryptophytes that develop long, thin, horizontally branching and rather shallowly penetrating underground rhizomes terminating at ground level as rosettes. These rosettes become dormant during winter and carry buds that resume growth the following year. Plants of *nevadensis* therefore spread laterally underground and form low mats from 1 to 2 cm. high and as much as a meter across in a 10-year period under good garden conditions. As the rhizomes become older they tend to increase a little in thickness and to become woody, but they never approach in height the crown system of *reflexa* to which they are homologous. These differences between the root and crown systems of *nevadensis* and *reflexa* are illustrated in figure 6 on page 17.

In the cross Timberline (without crown) × Oak Grove (with crown), the first-generation hybrid plants were definitely intermediate, combining characteristics from both parents. They developed some rhizomes, showing the influence of the subalpine parent, together with vertical, short, woody crowns, features obviously inherited from the foothill parent.

In the selfed second generation a complete range of recombinations of the parental characteristics appeared, most of the plants being in intermediate classes. The grading of the F_2 into classes was made on the basis of measurements of crown height on 10-year-old plants grown in the Mather garden.

The measurement of the height of the rosette buds above ground is subject to

some error because of irregularities in the ground level in a cultivated garden. Plants with a crown 2 cm. or less above the ground were placed in one extreme group and were comparable with the Timberline parental type. At the other extreme were plants with crown buds 9 to 13 cm. above the ground, which included plants more or less comparable with the Oak Grove parent. The remainder of the population, consisting of an array of individuals with crowns between 3 and 8 cm. above ground, was placed in a third, intermediate group. It is doubtful whether any plants with winter buds exactly at the ground level like the true alpine type were segregated, and none equaled the crown height of the foothill parent.

Among the 434 F_2 individuals that survived after 10 years, 31 were in group 1, 306 in the intermediate group, and 97 in group 3, which approached the foothill *reflexa* type. Many forms intermediate between robust cushion plants (rosette chamaephytes) and matted near-hemicryptophytes were segregated.

The plants were not grown in the Stanford garden long enough for segregation for crown height in the F_3 to be studied, since only plants more than 5 years old express this character adequately.

The principal conclusion that can be drawn is that genes for crown height, for presence or absence of rhizomes, for thick as compared with thin rhizomes, and for horizontal as compared with erect branching either above or below ground level may be recombined in the F_2. The pattern of segregation indicates that the inheritance of life form is complex and is the resultant of the co-ordination of several characteristics each of which is probably regulated by several genes.

12. Anthocyanin

In most foothill forms of *reflexa* and in many coastal forms of *typica,* at all three transplant stations, the stems and veins of the leaves are heavily red or purple. In contrast, the alpine and subalpine races of subspecies *nevadensis* show no reddish purple sap color when grown in gardens at Stanford or Mather, except for traces at the point of attachment of the rosette leaves. In the Timberline garden, however, the plants of *nevadensis* become reddish in various shades, and members of the two lower-altitude subspecies become dark purple; nevertheless, even at the alpine station the most heavily colored forms of *nevadensis* are, on the average, lighter-colored than the least anthocyanous individuals of *reflexa* and *typica.*

The inheritance of anthocyanin coloration was studied in the two hybrids Timberline × Oak Grove and Upper Monarch Lake × Santa Barbara, and was found to differ somewhat. Data from the cross Timberline × Oak Grove are the more complete because the F_3 was studied, and it will therefore be discussed first.

Timberline × Oak Grove. The first-generation hybrid of the cross Timberline (green) × Oak Grove (highly anthocyanous) was intermediate between the parents. At the Timberline station it is more highly colored than at the lower altitudes of Stanford and Mather, but it remains intermediate at all stations.

In the second generation the segregation ranged from wholly green to highly anthocyanous. A few plants were segregated that were even less anthocyanous than the Timberline parent. These remained green at Timberline also.

The second-generation individuals were classified into five groups (table 28) on the basis of observations made over a period of years on the cloned transplants at the three stations, as follows: Class 1, plants that were green at Stanford, some of which became anthocyanous at Timberline; others remained green at all three stations and were therefore less anthocyanous than the alpine parent. Class 2, plants showing a trace of anthocyanin at Stanford and Mather, most of which became moderately to highly colored at Timberline; a small number were but faintly colored at all three stations. Class 3, plants intermediate at Stanford, like the F_1 hybrid. Class 4, plants fairly anthocyanous even at Stanford. Class 5, plants highly anthocyanous at all three stations and similar to the Oak Grove parent. The grouping was fairly strict in classes 1 and 2, although even these two fairly easily definable groups evidently contained more than a single genotype. In the intermediate and highly colored classes, the limits were more difficult to determine.

TABLE 28

SEGREGATION OF ANTHOCYANIN IN F_2 PROGENY OF TIMBERLINE × OAK GROVE AT STANFORD

F_2 CULTURES		Frequencies within classes Green→Deeply anthocyanous					Totals
		1	2	3	4	5	
3186: Oak Grove × Timberline	Obs.	17	65	220	88	22	412
	Calc.	11.2	72.4	225.4	83.7	19.3	412.0
	Ratio	7	45	140	52	12	256
3187: Timberline × Oak Grove	Obs.	3	58	93	6	3	162
	Calc.	2.5	←	157.0	→	2.5	162.0
	Ratio	1	←	62	→	1	64

For genetic formulas, see table 29.

The second generation was composed of the offspring of two selfed F_1 plants, one of each reciprocal cross. The segregation differed in the two progenies as shown in table 28. In culture 3186 (Oak Grove × Timberline), the frequency of F_2 individuals is distributed fairly symmetrically among the classes, and the frequencies of the extreme classes to the intermediates approach 1:14:1. In the reciprocal culture 3167, Timberline × Oak Grove, the frequencies in classes 2 to 4 are far from symmetrical, and the ratio of the plants in the extreme classes to the whole is approximately 1:64. It is therefore evident that the two F_1 individuals giving rise to the two F_2 progenies were genetically distinct.

Segregation in the F_3 progenies proved to be complex. Four progenies originating from selfed plants of 3186 segregated green plants in ratios of approxi-

mately 63:1, a fact that excludes a hypothesis assuming that the F_2 segregated in the ratio of 15:1. The assumption of linkage between multiple genes for anthocyanin followed by crossing-over would still further complicate this theory because it would require an increase in the number of assumed multiple genes. If linkage does exist, two multiple genes for anthocyanin could become incorporated in one chromosome through crossing-over. This, however, would increase the distinctness between the grades of anthocyanin, and no such effects were observed. Moreover, the observed segregations cannot be explained by assuming the action of inhibiting genes.

A theory that is to satisfy the observed results must take the following facts into account: (1) one parent (Timberline) is green at Stanford and Mather, but anthocyanous at Timberline; (2) F_2 plants that remain green at Timberline are segregated, a class transcending the alpine parent; (3) the progenies from the reciprocal F_2's differ (*a*) in their frequencies of greens, one having approximately a ratio of 15:1 and the other 63:1, and (*b*) in the symmetry of class frequencies in grades 2 and 4; and (4) although F_2 culture 3186 appears to segregate in the ratio 15:1, several of its F_3 progeny segregate in the ratio 63:1.

All the above considerations except 3*b* can be satisfied by assuming segregation in a system consisting of four pairs of multiple genes for anthocyanin, A_1 to A_4, and in addition one pair of complementary genes that activate the A_2 pair of multiples. The skewness (3*b*) in culture 3187 would, in addition, require the action of a pair of bleaching genes to counterbalance the multiple positive genes for anthocyanin. There is no further evidence to support this hypothesis.

Considerations 1 and 2 are satisfied if it is assumed that the Timberline parent is $a_1a_1a_2a_2a_3a_3A_4A_4$, that the Oak Grove parent is $A_1A_1A_2A_2A_3A_3a_4a_4$, and that the A_4 gene expresses itself fully only at Timberline, whereas at Stanford and Mather it reddens only the very base of the sheaths of the rosette leaves. The completely recessive genotype, $a_1a_1a_2a_2a_3a_3a_4a_4$, is the new class that is green at all three stations, and is obtained by transgressive segregation. Only three of the A genes, A_1 to A_3, operate at Stanford.

Considerations 4 and 3*a* are satisfied by assuming that one of the parents, probably Timberline, was heterozygous, C_2c_2, for the combination gene that activates A_2, and that the other parent was homozygous, C_2C_2. The F_1 plant 1442-1 would then be heterozygous for C_2 and at Stanford would segregate in the ratio 249:7 instead of 63:1. The reciprocal F_1 plant, 1443-2, would be homozygous, C_2C_2, segregating 63:1.

The F_2 ratios on the basis of the above hypothesis can be followed in table 29. The anthocyanin genes of the system form a kind of hierarchy, with the A_1 gene having the most penetrating effect in all three gardens. The A_2 gene is the next in strength, but needs the presence of C_2 for activation; the homozygous $A_2A_2C_2$ is moderately anthocyanous, whereas the heterozygous $A_2a_2C_2\cdots$ is only faintly anthocyanous at Stanford and Mather. In the absence of A_1 and A_2C_2, the weaker A_3 gene is able to express itself in plants that also are faintly anthocyanous at Stanford and Mather and moderately to strongly

anthocyanous at Timberline, and this biotype was at Stanford classified together with other faintly anthocyanous plants having one activated A_2 gene. The A_4 gene, finally, expresses itself only in the absence of all the other genes of the A series, and conspicuously only at Timberline. The theoretical F_2 ratio

TABLE 29

THEORY OF INHERITANCE OF ANTHOCYANIN IN F_2 PROGENY OF TIMBERLINE × OAK GROVE

Timberline, 1113-6 ——————×—————— Oak Grove, 1127-1

$a_1a_1a_2a_2C_2c_2a_3a_3A_4A_4$ $\qquad$ $A_1A_1A_2A_2C_2C_2A_3A_3a_4a_4$

F_1, 1442-1: $A_1a_1A_2a_2C_2c_2A_3a_3A_4a_4 = 3186$ in F_2

1443-2: $A_1a_1A_2a_2C_2C_2A_3a_3A_4a_4 = 3187$ in F_2

Genotypes				Phenotypes: Anthocyanin at Stanford	Ratio	Class
192 A_1	64 A_1A_1	36 A_2C_2	12 $A_1A_1A_2A_2C_2$	12 dark	12	5
			24 $A_1A_1A_2a_2C_2$	24 fairly dark	52	4
		28 a_2a_2 or $A_2c_2c_2$		28 fairly dark		
	128 A_1a_1	72 A_2C_2	24 $A_1a_1A_2A_2C_2$; 48 $A_1a_1A_2a_2C_2$	72 moderate	140	3
		56 a_2a_2 or $A_2c_2c_2$		56 moderate		
64 a_1a_1		36 A_2C_2	12 $a_1a_1A_2A_2C_2$	12 moderate		
			24 $a_1a_1A_2a_2C_2$	24 faint	45	2
		28 a_2a_2 or $A_2c_2c_2$	7 $a_1a_1a_2a_2$ or $A_2c_2A_3A_3$; 14 $a_1a_1a_2a_2$ or $A_2c_2A_3a_3$	21 faint		
			7 $a_1a_1a_2a_2a_3a_3$ $\{A_4, a_4a_4\}$	7 green	7	1
Total				256*	256	

A_1: anthocyanous under all conditions; darkest color, epistatic over all A genes except A_2.

A_2: anthocyanous only in the presence of the activating gene C_2; next darkest color.

A_3: faintly anthocyanous at Stanford and Mather, moderate to dark at Timberline.

A_4: green at Stanford and Mather, moderately anthocyanous at Timberline; hypostatic in the presence of A_1, A_2C_2, or A_3.

$a_1a_1a_2a_2a_3a_3a_4a_4$: green at all stations.

C_2: complementary gene which activates A_2.

* The ratios are computed on a four- rather than on a five-gene basis because A_4 is expressed only at Timberline.

at Stanford of 7:45:140:52:12 is fairly close to the observed ratio in culture 3186 as shown in table 28.

The F_3's originating from F_2's of culture 3186 listed in table 30 are also in good agreement with the theory. There is one large progeny segregating in the ratio 249:7, three 63:1, four 15:1, and three 3:1. Three progenies did not segregate any green plants but ranged over the remainder of the scale, and

TABLE 30

SEGREGATION OF ANTHOCYANIN IN F_3 PROGENY OF TIMBERLINE × OAK GROVE AT STANFORD

F_2 parents			F_3 progeny, frequencies						
Plant no.	Class	Genotypes		Dark	Fairly dark	Moderate	Trace	Green	Totals
3186-118	3	$A_1a_1A_2a_2CcA_3a_3$	Obs.	←		290	→	10	300
			Calc.			291.8		8.2	300.0
			Ratio			249		7	256
-123	3	$A_1a_1A_2a_2CCA_3a_3$	Obs.	←		61	→	1	62
			Calc.			61.02		0.98	62.0
			Ratio			63		1	64
-315	3	$A_1a_1A_2a_2CCA_3a_3$	Obs.	←		435	→	3	438
			Calc.			431.3		6.7	438.0
			Ratio			63		1	64
-405	3	$A_1a_1A_2a_2CCA_3a_3$	Obs.	←		300	→	2	302
			Calc.			297.3		4.7	302.0
			Ratio			63		1	64
-351	3	$A_1a_1a_2a_2\cdot\cdot A_3a_3$	Obs.	←		328	→	21	349
			Calc.			327.2		21.8	349.0
			Ratio			15		1	16
-545	3	$A_1a_1A_2a_2CCa_3a_3$	Obs.	←		18	→	2	20
			Calc.			18.7		1.3	20.0
			Ratio			15		1	16
-198	3	$a_1a_1A_2a_2CCA_3a_3$	Obs.	0	←	35	→	2	37
			Calc.			34.7		2.2	37.0
			Ratio			15		1	16

-391	3	$a_1a_1A_2a_2CCA_3a_3$	Obs.	0	←	22 —	8 →	3	33
			Calc.			22.7	8.2	2.1	33.0
			Ratio			11	4	1	16
-28	3	$A_1a_1a_2a_2 \cdot\cdot a_3a_3$	Obs.	←		18 →	0	3	21
			Calc.			15.7		5.3	21.0
			Ratio			3		1	4
-265	4	$A_1a_1A_2a_2CCA_3A_3$	Obs.	←		444 —	7 →	0	451
-387	4	$A_1a_1A_2a_2CCA_3A_3$	Obs.	←		331 —	12 →	0	343
			Calc.			321.6	21.4		343.0
			Ratio			15	1		16
-365	5	$A_1a_1A_2A_2CCA_3A_3$	Obs.	←	227 →	0	0	0	227
-473	2	$a_1a_1a_2a_2 \cdot\cdot A_3a_3$	Obs.	0	0	0	38	6	44
			Calc.				33.0	11.0	44.0
			Ratio				3	1	4
-484	2	$a_1a_1a_2a_2 \cdot\cdot A_3a_3$	Obs.	0	0	0	14	5	19
			Calc.				14.3	4.7	19.0
			Ratio				3	1	4
-235	1	$a_1a_1a_2a_2 \cdot\cdot a_3a_3$	Obs.	0	0	0	0	16	16
3187-65	3	$A_1a_1A_2a_2CCA_3A_3$	Obs.	← 47		176	→	0	223
			Calc.	55.7		167.3			223.0
			Ratio	1		3			4
-89	3	$A_1a_1A_2a_2CCA_3A_3$	Obs.	←		170	→	0	170
-6	3	$a_1a_1A_2a_2CCA_3A_3$	Obs.	0	← 41	76	→	0	117
-5	1	$a_1a_1a_2a_2CCa_3a_3$	Obs.	0	0	0	0	17	17
-425	1	$a_1a_1a_2a_2CCa_3a_3$	Obs.	0	0	0	0	39	39

For explanation of gene symbols see table 29.

produced only anthocyanous offspring. The nine F_2 parents classified as having grade 3 anthocyanin all segregated greens, but in different ratios. Two F_2's of class 2 segregated only faintly anthocyanous and green F_3 progeny in the ratio 3:1, and two F_2 plants of class 4 segregated plants ranging through the anthocyanin scale, but no greens. The progeny of one darkly anthocyanous F_2 plant, of class 5, -365, ranged only from dark to fairly dark, and the green F_2 plant, of class 1, -235, produced only green F_3's. The two green F_2 plants of culture 3187 also produced green F_3's only.

The proposed gene system serves to explain in terms of genetic theory the F_2 ratios and the rather confusing array of segregations in the F_3 progenies. It is not the only possible explanation. The degrees of freedom are limited, however, because the F_2's were classified in three contrasting environments, and a reasonable number of F_3 progenies were available for study, so that the observed ratios of many progeny tests have been taken into account. It is possible that genes other than the A_2 for anthocyanin require activation by combination genes, but if so the parental races must both have been homozygous for these combination genes.

Upper Monarch Lake × *Santa Barbara.* A somewhat different situation was found in the cross Upper Monarch Lake (green) × Santa Barbara (strongly anthocyanous). The F_1 plants of both reciprocals were highly anthocyanous in the stems and veins of the leaves, like the Santa Barbara parent, thereby showing strong dominance of this character.

The dominance was also evident in the F_2 inasmuch as nearly three-fourths of the progeny were classified as moderately to strongly anthocyanous, and approximately one-fourth as slightly anthocyanous to green. This apparently simple ratio was deceptive, however, for the slightly anthocyanous plants do not belong with the greens; the truly green plants constituted only approximately one-eighth of the total.

The F_2 plants were grouped into seven classes according to anthocyanin coloration, ranging from entirely green to highly anthocyanous. This classification was made only once in the Stanford garden, and the listing is therefore subject to the usual uncertainties in classifying such a quantitative character. The frequencies in the various classes are listed in line 12 of table 9 (p. 41).

The F_2 plants of class 1 had no trace of anthocyanin; they were greener than the alpine Upper Monarch Lake parent, and would be expected to remain green even if planted at Timberline. Class 2 included plants that also were green but contained traces of anthocyanin at the base of the leaf sheaths of the basal rosette, like the alpine parent; plants of this group could be expected to become moderately anthocyanous at Timberline, like Monarch Lake. Class 3 plants were faintly anthocyanous on the leaf blades and graded into class 4, containing slightly anthocyanous plants. Classes 5 and 6 were moderately to strongly anthocyanous, and class 7 was composed of deeply anthocyanous plants matching the Santa Barbara parent.

The two green classes, 1 and 2 (table 31), which, together, correspond to

class 1 in the cross Timberline × Oak Grove, were the most easily distinguishable in the F_2 and provide the key to an understanding of the cross between the alpine and Coast Range races. The green plants of class 1 are recessive for all A genes; those of class 2, which have colored bases on the sheaths of the rosette leaves, appear to possess the A_4 gene.

One anthocyanin gene which acts as a semidominant is evidently involved in the cross Upper Monarch Lake × Santa Barbara. This gene is probably more dominant than the A_1 gene in the first cross. For simplicity, this semidominant

TABLE 31

SEGREGATION OF ANTHOCYANIN IN F_2 PROGENY OF UPPER MONARCH LAKE × SANTA BARBARA

Upper Monarch Lake, 1134-1 ——————×—————— Santa Barbara, 1119-1

$a_1a_1 \cdot\cdot a_3a_3c_3c_3A_4A_4$ $A_1A_1 \cdot\cdot A_3A_3C_3C_3a_4a_4$

F_1, 3300-3: $A_1a_1 \cdot\cdot A_3a_3C_3c_3A_4a_4$

CLASSIFICATION OF F_2, 4059

Phenotypes					Genotypes
Class	Anthocyanin intensity	Frequencies: Observed	Frequencies: Calculated	Frequencies: Ratio	
1	entirely green	36	27.2	7	$a_1a_1a_3a_3 \cdot\cdot a_4a_4$ plus $a_1a_1A_3 \cdot cca_4a_4$
2	green, bases of sheaths red	90	81.7	21	$a_1a_1a_3a_3 \cdot\cdot A_4$ plus $a_1a_1A_3 \cdot ccA_4$
3, 4	slight	155	140.1	36	$a_1a_1A_3 \cdot C \cdots$
5–7	moderate to strong	715	747.0	192	$A_1 \cdots\cdots$
	Total	996	996.0	256	

A_1: dominant gene for strong anthocyanin.

A_3: gene causing light anthocyanin in leaves and stems; activated by C_3, a combination gene specific for A_3.

A_4: gene which, at Stanford, causes plant to be green except that the very bases of the sheaths of the rosette leaves are red; would be anthocyanous at Timberline.

Plants recessive for all three genes have no trace of anthocyanin.

gene in table 31 has also been listed as A_1. The segregation in the F_2 progeny of this hybrid furthermore suggests the presence of a combination gene, C_3, activating the A_3 gene for faint anthocyanin instead of the stronger A_2 gene. In Monarch Lake × Santa Barbara the A_2 gene seems to be either absent or unactivated.

On the basis of these assumptions, and by adding classes 5 to 7 and 3 to 4 together, the groups of F_2 individuals of Upper Monarch Lake × Santa Barbara approach a theoretical ratio of 192:36:21:7. This ratio fits a segregation governed by a system of four pairs of genes as indicated in table 31. The absence of data from F_3 cultures makes it impossible to check the correctness of

this hypothesis, but it falls in line with the data from the cross between Timberline and Oak Grove, as well as accounting for the type of segregation observed in the F_2.

The combined evidence from the two crosses indicates clearly that the presence or absence of anthocyanin in three subspecies of *Potentilla glandulosa* is controlled by fairly complex systems of genes consisting of components differing in strength, that some genes require complementary genes to activate them, that some genotypes can be recognized only in certain kinds of environment, and that probably most segregating genotypes alter the expression of their phenotype with the climate. Transgressive segregation occurred through the recombination of genes introduced from genetically contrasting parental races.

13. Pubescence

One of the prominent differences among the subspecies of *Potentilla glandulosa* lies in the kind and amount of pubescence that they have. In the cross Upper Monarch Lake (subspecies *nevadensis*) × Santa Barbara (subspecies *typica*), studies were made on the segregation of this character in F_2 progeny.

The herbage of the Santa Barbara form of *typica* is densely covered with stalked, exuding glands interspersed with many long and somewhat shaggy hairs. The alpine Upper Monarch Lake form of *nevadensis,* on the other hand, is almost glabrate, having few, scattered thin hairs and no or very minute glands. In the wild, many intermediates exist between these extremes.

The first-generation hybrid between the alpine and the coastal plant is glandular-pubescent, but not as strongly as the coastal parent. In the F_2 resulting from self-pollination of one F_1 plant, there was wide segregation of types, ranging from individuals as pubescent and glandular as the *typica* parent to a single glabrescent plant that approached, but did not match, the *nevadensis* parent. No attempt was made to differentiate between glandular and hairy pubescence, for they seem to be strongly correlated. The six degrees of pubescence recognized in the classification of the F_2 population are listed in table 32.

As is indicated in the table, more than three-fourths of the F_2 individuals were in classes 5 and 6, class 6 representing the type of the Santa Barbara parent. At the opposite extreme, no plants were found in class 1 representing the Monarch Lake parent, only 1 in class 2, and 20 in class 3 (fairly glabrescent). The distribution of the F_2 plants is therefore highly skew, and it is also noteworthy that no F_2 individuals exceeded either of the parents in the expression of this character.

These facts suggest that the inheritance of pubescence may be fairly simple. The glandular-pubescent characteristic of the *typica* parent is highly dominant over the glabrateness of *nevadensis.* The high frequencies in classes 5 and 6 would suggest the presence of a fairly dominant and epistatic gene for glandular pubescence, G_1. The attenuation in the frequencies toward the glabrate end of the range of variation could be produced through segregation of a series of

genes for glandular pubescence, as, for example, G_2 to G_5, of decreasing strength, so that the stronger genes cover the effects of the weaker, and cause each gene to be epistatic over the next in the series. According to this hypothesis the homozygous recessive, $g_1g_1g_2g_2g_3g_3g_4g_4g_5g_5$, would be the nonglandular, glabrate *nevadensis* form. The expected frequencies in a system of five pairs of genes that are successively epistatic over one another are calculated in table 32 for the F_2 population of 970 individuals and compared with the observed frequencies.

That the agreement between calculated and observed ratios is far from perfect is not surprising, because the transition between the classes was gradual, so that accurate grouping was difficult. On the basis of the present data it is

TABLE 32

INHERITANCE OF GLANDULAR PUBESCENCE IN F_2 PROGENY OF UPPER MONARCH LAKE × SANTA BARBARA

Phenotypes					Genotypes
Class	Degree of glandular pubescence	Frequencies: Observed	Frequencies: Calculated	Frequencies: Ratio	
1	glabrate (P_1 type)	...	0.9	1	$g_1g_1g_2g_2g_3g_3g_4g_4g_5g_5$
2	glabrescent	1	2.8	3	$g_1g_1g_2g_2g_3g_3g_4g_4G_5\cdot$
3	fairly glabrescent	20	11.4	12	$g_1g_1g_2g_2g_3g_3G_4\cdots$
4	fairly pubescent	174	227.4 { 45.5	48	$g_1g_1g_2g_2G_3\cdots\cdots$
			181.9	192	$g_1g_1G_2\cdots\cdots\cdots$
5	pubescent (F_1 type)	599	485.0	512	$G_1g_1\cdots\cdots\cdots$
6	very pubescent (P_2 type)	176	242.5	256	$G_1G_1\cdots\cdots\cdots$
	Total	970	970.0	1024	

G_1 to G_5: multiple genes for glandular pubescence in decreasing order of strength (epistasis).

possible only to estimate that a five- or a six-gene system may be involved. An analysis of F_3 and F_4 populations would be required to clarify our understanding of the inheritance of pubescence beyond this point.

Apparently neither inhibitors nor complementary genes were involved in the segregation of this character, because no plants exceeded either parent in degree of pubescence. The hereditary system therefore probably consists of genes of the multiple type that differ only in penetrance, the degree with which they express themselves.

14. Length of Leaves

The striking differences between the lengths of the small leaves of subspecies *nevadensis* and the much larger ones of *typica* or *reflexa* have been described and illustrated in chapter I. The variations within and between local populations of each subspecies are such that overlapping, intergrading variation re-

sults, emphasizing the quantitative nature of this character. Leaf size is closely correlated with the growth rate of the plant, and strong modifications due to the effects of differences in environment are superimposed on genetic differences.

Upper Monarch Lake × *Santa Barbara.* When the alpine Upper Monarch Lake form, having small leaves, is crossed with the large-leaved coastal Santa Barbara parent, the F_1 progeny have leaves even slightly larger than those of Santa Barbara. In the F_2 the segregation is extreme, transcending the limits of both parental types and the F_1. The frequency distribution of the leaf lengths is shown in figure 18, which is based on measurements of the largest leaf of each

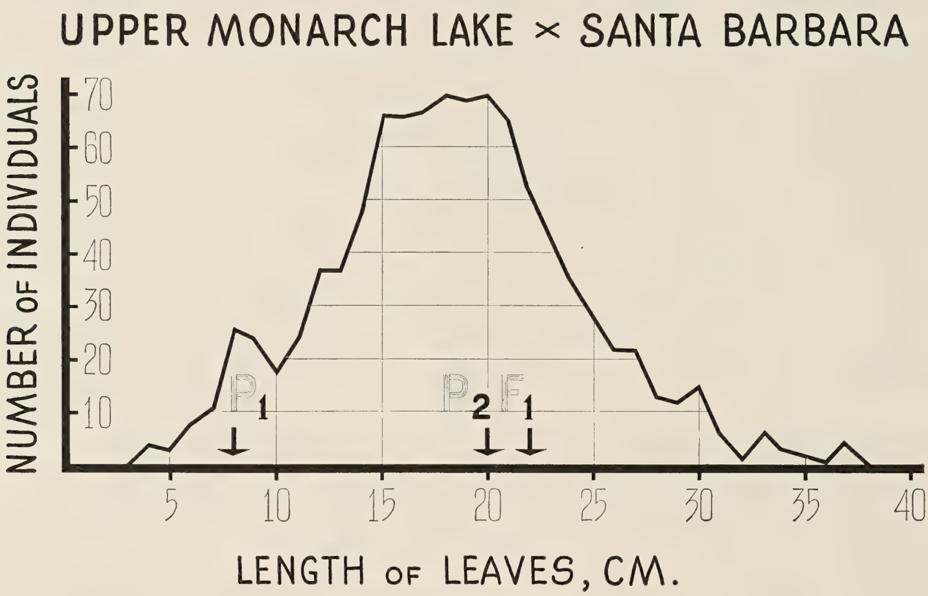

Fig. 18. Frequency distribution of lengths of longest rosette leaves among 996 F_2 progeny of Upper Monarch Lake × Santa Barbara.

All the plants were grown in the same garden at Stanford. Note the transgressive segregation as compared with the parents.

of 996 F_2 individuals and of the parents. The transgressive nature of the segregation is especially noticeable among the large-leaved offspring, nearly one-fourth of the F_2 plants having leaves larger than either the coastal parent or the F_1.

It would be futile to attempt to estimate the number of genes that regulate the inheritance of leaf length in this cross. The gene system determining leaf length is more complex than the system controlling pubescence. The transgressive segregation indicates either that the alpine and coastal parents have different genes in a multiple series for leaf length, or that they possess genes of the complementary type, or that they differ in inhibitors that counteract genes with positive effect, or that a combination of such factors is operating. In the absence of data from F_3 or later generations it is impossible to arrive at satisfactory deductions regarding any of these possibilities.

Timberline × Oak Grove. A rather similar genetic situation was found in the cross between the small-leaved subalpine *nevadensis* from Timberline and the large-leaved foothill form of *reflexa* from Oak Grove. The F_1, however, had a smaller leaf size than the lowland parent, not larger, as in the preceding cross. The length of the F_1 leaves was not intermediate between the parents, but closer to the length in the large-leaved foothill Oak Grove parent.

In the F_2 there was transgressive segregation in the direction both of small and of large leaves, and, unlike the F_2 progeny of Monarch Lake × Santa Barbara, the frequency of Stanford-grown plants was weighted in the direction of small-leaved individuals. The frequency curves of the same 502 cloned F_2 individuals grown at the Mather and Timberline transplant stations assume different shapes, however. See figure 19, which also demonstrates the changed relations between parents, F_1, and F_2 in the three environments.

At Stanford and Mather the Oak Grove foothill parent, 1127-1, has longer leaves than the subalpine parent, 1113-6, or than the F_1, but at Timberline the positions are reversed: the subalpine parent that is native there, and the F_1, have slightly longer leaves than the foothill plant, which, in the alpine environment, is highly modified and normally dies except for an occasional transplant that survives for a year or two among repeated trials. The three frequency diagrams in figure 19 are so different that they simulate curves of three genetically distinct populations. The Mather diagram differs especially from the other two.

Not only do the frequency curves for the entire cloned F_2 population differ radically from station to station, but also there are complex station-to-station responses of individual plants. This complexity is illustrated by the lengths of leaves of seven pairs of clones listed in table 33. In each pair of individuals the leaf lengths at Stanford are the same, but the lengths of the two become different at Mather and change their relative positions again at Timberline. This three-dimensional variation repeats itself over the entire range from the pair of plants having small leaves (6 cm.) at Stanford to plants having the largest leaves (24 cm.).

Gene-initiated balances between enzymatic and related physiological processes probably differ in the three contrasting environments. Evidence that a gene may become activated in only one of the three environments was found in the gene A_4 for anthocyanin, which expresses itself only at Timberline. Likewise, as was pointed out in the discussion of the characters notch, flower color, and petal size, inhibiting genes appeared to have greater penetrance, that is, greater effect, at the lower than at the higher altitudes. It is probable that some of the modifications are produced by differences in the relative speeds of the physiological processes under contrasting temperatures, and that other modifications arise because different complements of genes become activated in a different environment.

The observation that genes determining leaf length at Stanford, Mather, and Timberline probably are, at least in part, not the same is an important one. It seems futile to go beyond this point and attempt to determine the number of

genes that regulate leaf size in the foothill as contrasted with the subalpine races of *Potentilla glandulosa.* The transgressive segregation suggests the presence of inhibitors and complementary genes.

On the basis of the shape of the curves and the degree of transgression, one

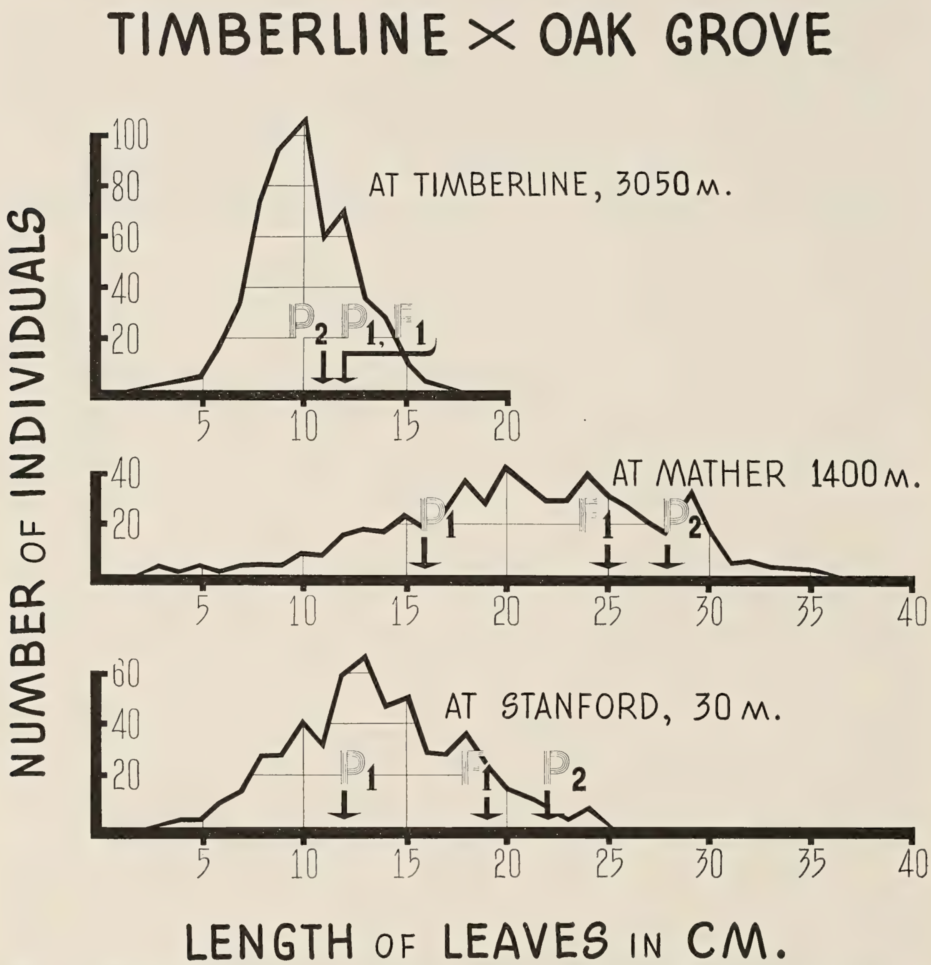

FIG. 19. Frequency distribution of lengths of longest rosette leaves among 502 F_2 progeny of Timberline × Oak Grove cloned and grown at the Stanford, Mather, and Timberline transplant stations.

Note transgressive segregation in all three environments as compared with the parents, and the shifts in direction of transgression from station to station.

would estimate that possibly between five and ten pairs of genes govern the inheritance of leaf length at any one station. Some of the genes for leaf length doubtless function at more than one station. Since each of the three transplant stations seems to bring into operation a different combination of genes, an estimate of the minimum total number responsible for the inheritance of leaf

length is higher than if the expression were the same in all environments. It seems probable that more than ten but fewer than twenty pairs of genes determine this character in the three environments. A significant positive correlation that exists between leaf lengths at Stanford and Mather suggests that a large proportion of the genes have a similar influence in the two environments.

TABLE 33

Leaf lengths of cloned F_2 plants of Timberline × Oak Grove at three altitudes. Measurements in centimeters.

Clone no.	At Stanford, 30 m.	At Mather, 1400 m.	At Timberline, 3050 m.
-14	6	20	11
-264	6	9	5
-225	9	7	10
-80	9	33	11
-357	11	5	9
-506	11	29	15
-425	13	13	16
-317	13	38	13
-115	15	8	8
-569	15	27	15
-440	22	17	9
-22	22	31	14
-402	24	21	13
-189	24	32	10

15. Number of Leaflets on Leaves Subtending the Inflorescence

Another character that distinguishes races of *Potentilla glandulosa* is the degree to which the leaves subtending the inflorescence have been differentiated from the other cauline leaves. The inheritance of this characteristic was investigated only in the cross Upper Monarch Lake, subspecies *nevadensis,* × Santa Barbara, subspecies *typica.* In *nevadensis* the leaves at the base of the inflorescence mostly consist of only 3 leaflets much reduced in size, whereas in *typica* the corresponding leaves scarcely differ from the others of the cauline region and have 5 to 7 large leaflets at the base of the inflorescence and 3 leaflets above.

The F_1 hybrid had relatively large subtending leaves with 3 to 5 leaflets, resembling those of Santa Barbara but not so large. In the F_2 the segregation ranged from plants having 3 small leaflets throughout the inflorescence region to plants with 5 to 7 larger leaflets. An attempt was made to classify the F_2 individuals in three classes, as follows: (1) plants with 3 leaflets throughout the inflorescence region; (2) those with 5 leaflets at the base of the inflorescence

and 3 leaflets above; and (3) plants having 7 leaflets at the base, 5 leaflets in the middle, and 3 leaflets above. The result is shown in table 34.

So much transition existed between classes 2 and 3 that the distinction between them became difficult. Approximately one-fourth of the F_2 progeny, 252 plants, had 3 small leaflets throughout the inflorescence (class 1), suggesting that subspecies *nevadensis* is recessive for one major pair of genes limiting the number of leaflets to 3. Conversely, *typica* possesses the dominant counterpart of this pair of genes, causing 5 to 7 leaflets to appear. Subspecies *typica* also seems to possess genes that cause bracts to become large and leaflike. In the absence of F_3 data, it is impossible to pursue the analysis further.

The character many leaflets is correlated with other sets of characters, especially with the congested type of inflorescence, late flowering, large sepals, dense pubescence, long rosette leaves, and large akenes, all of which are characters of the *typica* parent. Statistically, these correlations are highly significant, as is shown on pages 114 to 116.

TABLE 34

Segregation in number of leaflets in F_2 progeny of Upper Monarch Lake × Santa Barbara

Class	No. of leaflets	Frequencies		
		Observed	Calculated	Ratio
1	3	252	243.0	1
2	5	584	486.0	2
3	7	136	243.0	1
Total	15	972	972.0	4

In conclusion, it appears that differences in leafiness of the bracts are governed by relatively simple gene systems. Some of these genes, moreover, are located in chromosomes that also contain genes controlling other characteristics of the herbage and inflorescence.

16. Stem Length

Perhaps the most obvious character differentiating the various races and subspecies of *Potentilla glandulosa* is the length of the flowering stems. The short-stemmed alpines of *nevadensis* contrast markedly with the tall forms of *reflexa* from middle and lower altitudes, as was described in chapter I. Almost as great is the contrast between *nevadensis* from high altitudes and *typica* from the Coast Ranges.

Stem length is a quantitative character that, like leaf length, can be easily measured. Both characters are subject to marked modifications by environment, so that their expression at any given place is the result of the interplay between

heredity and environment. The influence of these factors is so well balanced that the phenotype is controlled by both to an almost equal degree.

The purpose of the present study is twofold: (1) to determine approximately the kind of gene system that governs hereditary differences between the climatic races of *Potentilla glandulosa,* and (2) to compare the effects of the genes with the effects of differences in environment.

Upper Monarch Lake × *Santa Barbara.* On the rare occasions when the dwarf Monarch Lake plant flowered at Stanford, its stems were only 9 cm. tall; those of the Coast Range plant from Santa Barbara averaged 54 cm. The F_1 hybrid was 60 cm. tall and clearly displayed hybrid vigor.

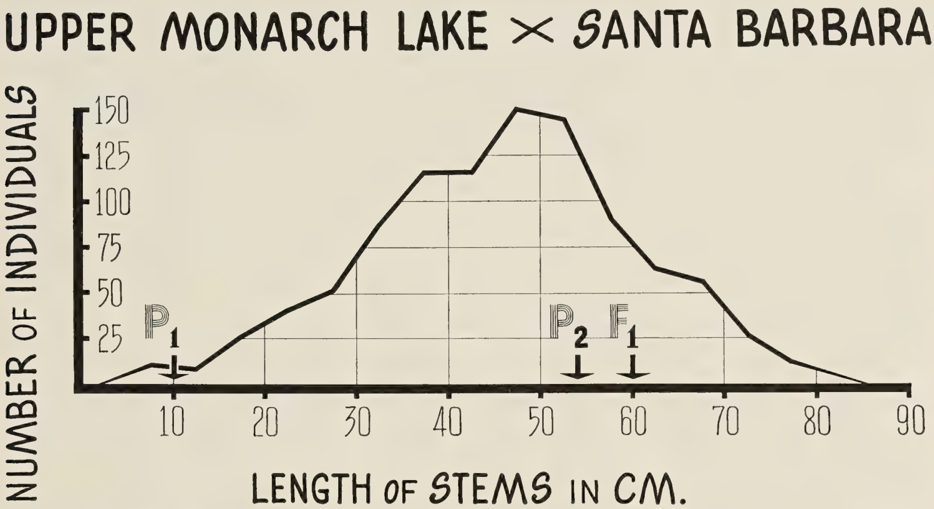

FIG. 20. Frequency distribution curves showing lengths of stems among 973 F_2 progeny of Upper Monarch Lake × Santa Barbara grown in a uniform garden at Stanford.

Note the strongly transgressive segregation toward long stems in both the F_1 and F_2 as compared with the parents.

Among the 973 F_2 progeny that flowered at Stanford the segregation ranged from dwarfs as short as the alpine parent to individuals much exceeding both the coastal parent and the F_1, as is shown by the frequency diagram, figure 20. Approximately 15 individuals in this population matched the alpine parent in stem length. This frequency may not truly reflect the number of genes involved, for the stems could scarcely be much shorter than those of the alpine parent when grown at Stanford, an unfavorable climate for this race. Transgressive segregation would therefore not be evident on the minus side of the frequency diagram. At the opposite extreme, approximately one-fourth of the progeny exceeded the coastal parent in stem length, and 155 exceeded the F_1. The occurrence of such transgressive segregation may indicate either that one parent had complementary genes activating genes possessed by the other parent, or that the two parents differed in the multiple-type genes governing stem length that they possessed.

In the absence of data from segregating F_3 progeny it is not possible to estimate the number of genes involved.

Timberline × *Oak Grove.* Data relating to the cross Timberline (subspecies *nevadensis* having short stems) × Oak Grove (subspecies *reflexa* having long stems) are more complete. The F_1 of this cross was tall, but did not exceed the long-stemmed Oak Grove parent.

The second generation segregated both short- and long-stemmed individuals over a continuous range that at Stanford somewhat exceeded both the parental extremes, as is indicated by the lowermost frequency distribution diagram in figure 21. In this F_2 population the class of highest frequency was shorter-stemmed than the F_1, and nearly intermediate between the parents. This situation is in contrast with the F_1 and F_2 of the cross Upper Monarch Lake × Santa Barbara, in which the F_1 exceeded the tallest parent, and the most frequent classes in the F_2 fell close to the tallest parent. It is therefore evident that the gene systems regulating stem length in the two crosses differ, and that hypostatic length-decreasing genes may be operating in the second cross.

The relative stem heights of the parents, F_1's, and F_2's of Timberline × Oak Grove in the three environments at Stanford, Mather, and Timberline are shown in figure 21. The frequency curves at the three stations differ markedly, especially when the relative position of the parents and the F_1 is considered. The Mather curve has the widest spread, and shows wide transgressive segregation in both directions. The tallest fraction at Mather is 15 cm. longer than the tallest parent, and the shortest-stemmed fraction is 20 cm. shorter than the alpine parent. One-third of the F_2 plants at Mather have shorter stems than the Timberline parent.

At Timberline the foothill parent is modified to a dwarf, and the relatively vigorous F_1 therefore becomes taller than either parent. Transgressive segregation at Timberline is in the direction of taller stems, approximately 100 plants exceeding both parents and the F_1. Although the foothill parent itself is unable to survive and develop normally at Timberline, it is able to transmit to its hybrid with the subalpine parent the ability to grow with considerably increased vigor.

There is a significant correlation between stem length of clones at one station and at another, especially between Mather and Timberline, as will be discussed more fully in later pages. The three frequency curves are therefore not independent despite the fact that they differ so widely. Nevertheless, the modifications in the three environments are striking, as is evident from the relative positions of the parents and the F_1, and the positions of individual clones within the F_2's at the three stations.

A sample consisting of 30 of the 575 clones is thus analyzed in table 35. This sample is arranged according to stem length at Stanford; two or three clones having approximately the same stem length at Stanford are listed in a group, permitting a comparison of their responses at the other two stations. Almost the entire range at each station is covered by this small sample.

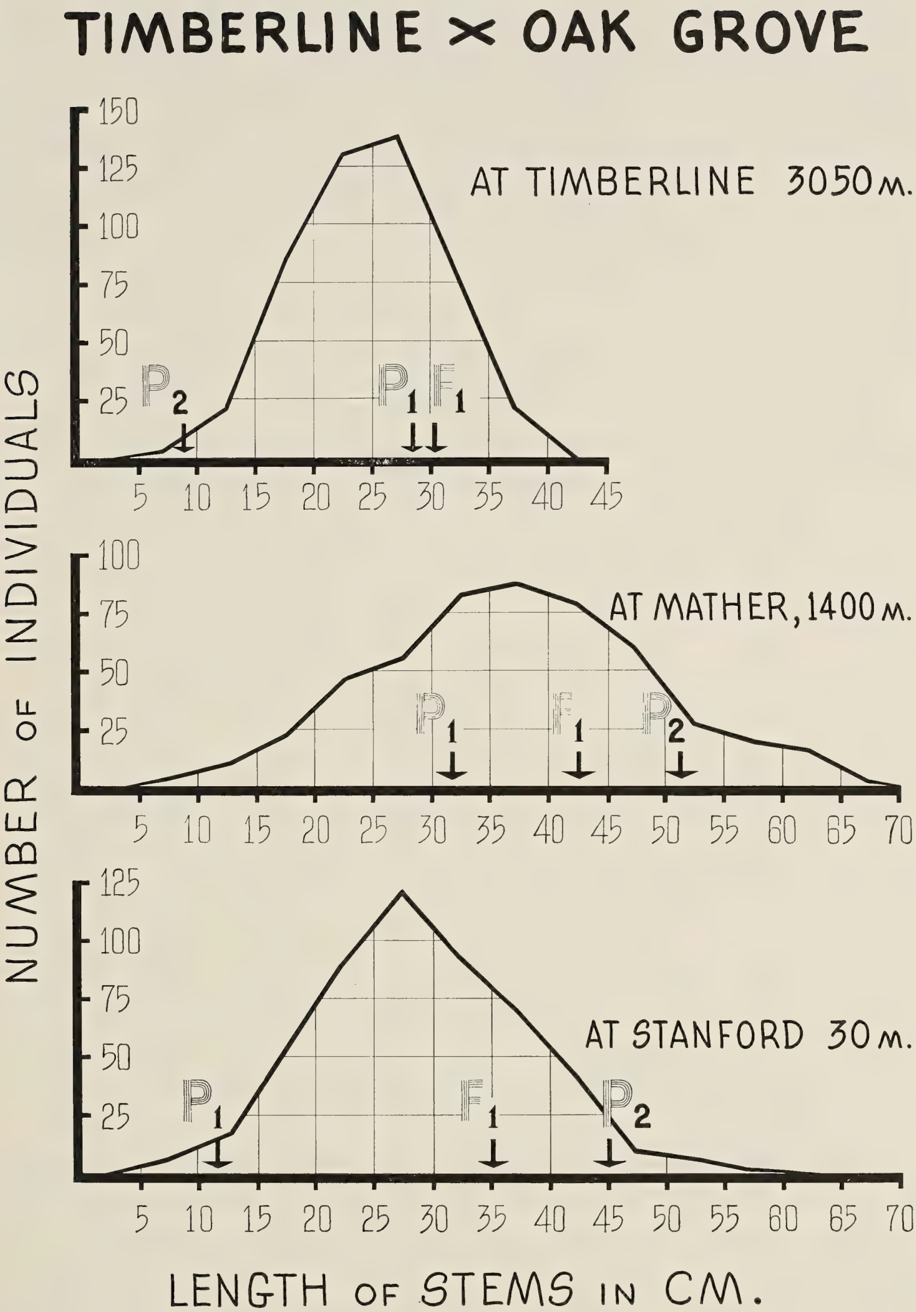

FIG. 21. Frequency distribution curves showing lengths of stems of 517 cloned F_2 progeny of Timberline × Oak Grove at the Stanford, Mather, and Timberline stations.

Note that both the extent and the direction of transgression differ in the three environments.

It can be seen from table 35 that the three clones -52, -230, and -484, all of which at Stanford have mean stem lengths of about 15 cm., at Mather have lengths ranging between 16.3 and 61.7 cm. and cover almost the entire gamut of variation. The group having stem lengths 21.0 to 21.7 at Stanford shows less divergence, but clone -454 of this group has stems of equal length at the three stations, whereas clone -541 is significantly taller at Mather than at the two other stations; in contrast, clone -254 is shorter at Mather than at either Stanford or Timberline.

TABLE 35

Stem lengths of cloned F_2 plants of Timberline × Oak Grove at three altitudes. The measurements (in centimeters) are averaged for 4 years at Stanford and at Mather, and for 8 years at Timberline.

Clone no.	At Stanford, 30 m.	At Mather, 1400 m.	At Timberline, 3050 m.	Clone no.	At Stanford, 30 m.	At Mather, 1400 m.	At Timberline, 3050 m.
-14	10.5	36.5	29.1	-23	25.3	36.7	38.1
-244	10.0	23.3	36.1	-99	25.5	61.7	36.7
				-540	25.3	20.7	11.0
-174	12.0	9.0	15.0				
-491	12.0	31.0	22.5	-73	27.3	60.7	19.3
				-156	27.7	27.3	25.1
-52	15.5	61.7	27.0	-253	27.7	50.3	40.1
-230	15.7	16.3	23.7				
-484	15.7	34.7	32.7	-91	32.5	54.0	14.5
				-432	32.3	50.3	34.3
-33	17.3	21.5	34.5	-444	32.7	31.3	30.4
-374	17.3	40.5	29.0				
-380	17.3	21.5	11.5	-317	35.3	36.7	36.6
-254	21.5	14.7	27.7	-108	43.3	44.5	20.8
-454	21.7	22.5	21.6	-118	43.7	60.3	29.8
-541	21.0	40.8	27.3	-315	43.5	38.3	43.0
-418	24.7	46.5	30.9	-385	53.7	32.0	19.0
-497	24.3	16.8	21.3	-405	53.3	51.8	29.8

Certain distinct patterns of response can be recognized from the sample of clones listed in table 35. Clones -244 and -33 are distinctly tallest at Timberline, decreasing in size at Mather and Stanford, but clone -385 was distinctly tallest at Stanford. Plants -174 and -497 are shortest at Mather, in contrast with -99 and -73, which are tallest at this altitude, whereas clones -444 and -317 have similar heights at all three stations. In this connection it should be remembered that both the parents are tallest at Mather, that Coast Range races of *typica* are tallest at Stanford, and extreme alpine plants of other species are tallest at Timberline. In recombining the genes of two individuals representing fairly con-

trasting races it has therefore been possible to obtain in the progeny a range of variability that exceeds the limits of the parent natural races.

The number of genes that control the inheritance of stem length at any one station is obviously large, and the manner in which the responses of the clones diverge from station to station is spectacular. The variations in response are not unlike the modifications in the characters notch and anthocyanin described in earlier pages, where the effects of certain genes could scarcely be observed at the lowland station. Considerable information on phenomena paralleling these observations is reported in genetic literature during the period in which the relation between the genotype and phenotype was emphasized, as for example, red flower color in *Primula sinensis* (Baur, 1914), and deep velvety purple color in a chromosome mutant of *Viola arvensis* (Clausen, 1926). In both these plants the color disappears at higher temperatures.

It is highly unlikely that all the possible genetic recombinations for stem length were realized in the F_2 population of Timberline × Oak Grove, which consisted of only 575 individuals. The transgressive segregations suggest the action of complementary and inhibiting genes. At Mather the position of the transgressive segregants on the minus side suggests that fairly recessive inhibitors are at play, and at Timberline transgressive segregants on the plus side indicate that complementary genes of positive effect are active.

Possibly at least five or six pairs of genes of the multiple type controlling stem length operate at each of the three stations in addition to complementary and inhibitory genes. At any one station the response of individual F_2 plants is fairly fixed from year to year except for minor variations caused by climatic differences between years, but the responses at one station do not provide a basis for predicting the response at another. The total number of genes controlling stem length in the cross Timberline × Oak Grove at the three environments may therefore range between ten and twenty pairs, probably closer to the higher figure.

Further evidence bearing on the inheritance of stem length in Timberline × Oak Grove is shown by the frequencies observed in F_3 progenies of 20 selfed F_2 plants of diverse lengths. These data are summarized in table 36, in which the progenies are arranged progressively according to their mean heights in the F_3. The class frequencies of the F_3's are given in intervals of 5 cm., and for comparison the average heights of the F_2 parent and its F_3 progeny are listed for the Stanford environment.

It is evident that in the F_3 there is no depression in height as compared with the parental strains. The average height of the tallest parent, 1127-1, was 45 cm. at Stanford, and several progenies had many plants exceeding this figure, some by as much as 30 cm. The progenies of -118, -387, -265, and -405 substantially extend beyond the limits of the whole F_2 population grown at Stanford and demonstrate that the F_2 population was too small to permit the realization of all the possible genetic recombinations.

TABLE 36

Segregation of stem length in F_3 progenies of Timberline × Oak Grove at Stanford

F_2 parent	Frequencies of stem length (class limits in cm.)																Means (cm.)	
	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–55	55–60	60–65	65–70	70–75	75–80	Totals	F_2 parent	F_3 progeny
-484	3	3	13	1	2	..	..	..	..	..	..	..	..	..	..	22	15.8	15.0 ± 1.2
-425	1	5	10	9	2	..	1	..	..	..	..	..	..	..	..	28	24.7	17.0 ± 1.0
-473	4	7	10	11	3	5	2	2	..	..	..	..	..	..	..	44	29.8	21.8 ± 1.5
-5	1	2	1	5	4	6	2	..	..	..	..	..	..	..	..	21	24.8	26.4 ± 1.9
-235	..	3	2	3	2	2	2	2	..	..	..	..	..	..	..	16	29.8	26.9 ± 2.6
-89	4	5	24	35	49	51	12	1	..	..	..	..	..	..	..	181	31.3	26.6 ± 0.2
-6	2	2	16	26	22	24	18	6	..	..	..	..	..	..	..	116	32.5	27.7 ± 0.8
-391	..	2	2	4	2	5	7	5	3	2	..	1	..	..	..	33	42.5	34.4 ± 2.0
-28	..	..	..	1	6	3	5	3	1	1	1	..	..	..	..	21	33.0	35.5 ± 2.1
-65	..	3	4	14	27	49	47	35	24	15	4	..	..	1	..	223	46.3	37.4 ± 0.7
-365	..	2	4	11	19	37	47	54	37	23	2	..	..	..	..	236	44.8	39.2 ± 0.6
-123	..	..	2	1	6	9	13	12	13	1	3	..	..	..	..	60	41.0	38.6 ± 1.1
-198	..	..	..	1	5	4	8	9	7	2	1	..	..	..	..	37	45.3	39.3 ± 1.4
-118	3	1	9	5	30	47	48	55	55	26	18	7	..	..	..	304	43.8	40.0 ± 0.6
-351	..	1	7	8	18	40	69	64	80	57	12	..	..	..	..	356	52.0	41.7 ± 0.5
-387	..	1	6	11	26	30	56	77	51	44	25	9	6	1	..	351	52.3	42.6 ± 0.6
-265	6	6	16	15	23	44	68	72	62	55	47	35	12	1	1	463	49.8	43.4 ± 0.6
-545	..	..	..	..	1	..	5	2	9	2	1	..	..	..	..	20	40.7	42.5 ± 1.8
-315	1	2	2	3	15	19	56	72	101	78	58	21	4	1	..	433	43.5	46.4 ± 0.5
-405	1	4	2	14	11	8	14	25	54	58	70	34	19	3	..	317	53.3	49.7 ± 0.7
Position of parents and F_1		P_1					F_1	P_2										

Only one or two of the shortest-stemmed F_3 progenies approached a modicum of homogeneity for stem length. The others still segregated almost as extensively as the F_2. The tallest F_3 progenies exceeded the tallest plants found in the F_2, and there is some indication that the potential maximum was not attained in the samples of 300 to 400 F_3 plants.

It would probably require selection through ten or more generations to develop a degree of genetic homogeneity comparable with that found in wild populations. Strongly segregating hybrid populations such as these, however, can provide adequate material for natural selection for developing races fitted for many climates. Judging from the responses of the F_2 parents (table 13, p. 53), one would expect to find among the progeny of plant -484, for example, individuals especially well fitted to alpine conditions. Likewise, the progenies of plants -315, -351, and -405 would probably give rise to strains fitting the California Coast Range climate, those of -65 and -118 to plants especially adapted for mid-altitudes, and -28 and -89 to races having a great range of tolerance.

From all the available evidence bearing on the inheritance of stem length in races of *Potentilla glandulosa* from the two crosses Upper Monarch Lake × Santa Barbara and Timberline × Oak Grove, it is apparent (1) that this character is controlled by multiple genes, including complementary genes and probably inhibitors, (2) that the parents differ in their gene complements in such a manner that transgressive segregation results, leading to a high degree of variability, and (3) that different sets of genes for stem length appear to become activated at the three transplant stations.

17. Winter Dormancy

A character directly related to seasonal periodicity is the degree of winter dormancy of plants. Alpine types consistently become dormant in midwinter, even in the mild Stanford climate, whereas the forms from the California coast are strongly winter-active. These fundamental differences reflect diverging physiological patterns essential for the survival of the races in their respective environments.

Upper Monarch Lake × Santa Barbara. In the cross between the strongly winter-dormant subspecies *nevadensis* from Monarch Lake and the fully winter-active subspecies *typica* from Santa Barbara, the first-generation hybrid was moderately winter-active. In mid-January, for example, when the Santa Barbara parent was in vigorous, active growth, having new leaves up to 17 cm. long, the alpine was dormant and the F_1 had new leaves 9 to 10 cm. long.

In the second generation the segregation ranged from plants as fully winter-active as the Santa Barbara parent to others as winter-dormant as Monarch Lake, with no evidence of transgressive segregation. Observations were made in the middle of January, and the F_2's were grouped into six classes according to their degree of winter activity at Stanford. Class 1 consisted of plants as dormant as the alpine, and class 6 of plants as active as the coastal parent. The intermediate class 4 corresponded to the F_1 and was the highest in frequency.

The results are shown in table 37. This table differs slightly from table 9 because in mid-January 22 plants were listed as being fully dormant and they were so marked, but it was later found that 8 of them were dead. The frequency of 14 entirely dormant plants among 975 F_2's corresponds to a ratio of 1:63, suggesting that three pairs of multiple genes may control the degrees of winter activity at Stanford. Classes 2 to 6 in table 37 are somewhat more arbitrary than class 1 because the transitions are gradual and range from plants with very slight activity to plants that in midwinter have leaves 15 to 20 cm. long.

From these data it cannot be determined whether the Santa Barbara parent possesses three pairs of positive genes governing active winter growth or whether activity in the Upper Monarch Lake plant is suppressed by three pairs of inhibitory genes. In either event the F_1 becomes heterozygous for the three pairs and would be intermediate; likewise, approximately 1 out of 64 of the second-generation progeny should become as dormant as the alpine parent, and a like

TABLE 37

Segregation in winter activity in F_2 progeny of Upper Monarch Lake × Santa Barbara at Stanford

Frequencies	Degree of winter activity, classes					Total
	1 Entirely dormant	2, 3 Almost to fairly dormant	4 Inter-mediate	5 Fairly active	6 Fully active	
Observed	14	178	601	139	43	975
Calculated (based on three multiple pairs of genes)	15.2	←	944.6	→	15.2	975.0

number as active as Santa Barbara. Both theories would also account for the intermediates having various degrees of activity in a fairly symmetrical frequency distribution.

The evidence, therefore, points to one of the simplest genetic situations observed in the study of the differences between climatic races. The absence of transgressive segregation is especially noteworthy.

Timberline × *Oak Grove*. Additional but less clear-cut evidence on the inheritance of winter dormancy is provided by the cross between the fully winter-dormant race of *nevadensis* from Timberline and the race of *reflexa* from Oak Grove, which also becomes dormant but for a shorter period. At Stanford, the Oak Grove form tends to cease growing during the period between late December and early February, and its leaves are easily killed by light frosts. The Timberline parent is more resistant to frost, but remains dormant at Stanford until early March.

In the F_1 and some of the F_2's the late fall leaves are fairly resistant to frost at Stanford and may remain more or less green during the winter months. None

of the F_2 plants of the present cross, however, produce new leaves during midwinter, as did the partially winter-active plants in the preceding cross. Classification of the F_2 plants for differences in length of dormant period was not attempted because of difficulties in distinguishing between classes. No transgressive segregation of winter-active plants was observed except for increased winter greenness apparently resulting from greater resistance to frost in some of the F_2's.

In selfed third-generation progenies observations on the greenness of plants were made during a fairly mild winter at Stanford. The growth in all of 2000 F_3 plants was arrested during midwinter, but the leaves of some were more resistant to frost than others. For this reason, some individuals appeared to remain winter-green although no growth took place. This apparent winter activity will be discussed later under the heading frost susceptibility.

Santa Barbara × Oak Grove. A third hybrid was made between the winter-active *typica* from Santa Barbara and the moderately winter-dormant Oak Grove *reflexa*. The F_1 hybrids were distinctly more winter-active than the F_1's of Upper Monarch Lake × Santa Barbara. Comparisons between the parental races and the F_1 hybrids of the three crosses when grown at Stanford are summarized below.

Parental combination	Winter status of F_1's
Santa Barbara, winter-active × Oak Grove, short-dormant	Winter-active
Upper Monarch Lake, long-dormant × Santa Barbara, winter-active	Moderately winter-active
Timberline, long-dormant × Oak Grove, short-dormant	Fairly short-dormant

The hybrid Santa Barbara × Oak Grove F_1 was distinctly the most winter-active of the three combinations, and Timberline × Oak Grove the least.

18. Frost Susceptibility

A characteristic of importance for the survival of alpine and subalpine plants of subspecies *nevadensis* in their native environments is their ability to continue active growth after a short period of moderate freezing temperatures, or to mature seed in flowers which, in early stages of development, have been subjected to a severe frost shock.

The short growing season at Timberline, extending from July 1 to approximately September 15, is usually interrupted by several frost periods during which minimal night temperatures may drop to as low as $-7°$ C., and occasionally even lower. The shortness of the season, aggravated by the intermittent frosts, frequently prevents even some of the native plants from maturing seed. As was previously emphasized (Clausen, Keck, and Hiesey, 1940), some plants from high altitudes succeed in maturing seed because they are resistant to sum-

mer and early fall frosts, and other species flower so early that the inflorescences mature before freezing temperatures occur.

Further study shows that some native subalpines are severely injured by very light frosts accompanied by temperatures no lower than $-3°$ or $-4°$ C., whereas others show no damage at these temperatures. Frost-susceptible species include *Veratrum californicum* Dur., *Lilium parvum* Kell., *Thalictrum fendleri* Engelm., *Senecio triangularis* Hook., and *Calamagrostis canadensis* Beauf. Frost-resistant species include *Gentiana simplex* Gray, *Aster occidentalis* Nutt., *Ledum glandulosum* Nutt., *Stipa columbiana* Macoun, and *Aconitum columbianum* Nutt. Stems of the last-mentioned may freeze solidly in ice and continue activity after thawing. The subalpine races of *Potentilla glandulosa* and *Achillea lanulosa* Nutt. are intermediate between these two groups of species with respect to cold resistance.

The subspecies of *Potentilla glandulosa* differ widely in their ability to withstand freezing weather while still in active growth during the summer and fall at Timberline. Members of subspecies *reflexa* are quickly injured by light frosts, whereas subalpine and alpine members of *nevadensis* are much more resistant. Plants of the Coast Range race, subspecies *typica,* are at least as resistant to cold temperatures as *nevadensis* native at Timberline, a fact consistent with the cool temperatures prevailing at the coast during the winter growing period when coastal forms are growing in their native habitat.

Timberline × Oak Grove. The basal rosette leaves of the parent from Timberline, 1113-6, tend to be killed by fall frosts, but inflorescences containing immature seeds remain uninjured and succeed in yielding viable ripe seeds. The Oak Grove parent, 1127-1, is highly susceptible to frost injury, and rosette leaves and inflorescences are easily killed at Timberline. The F_1 hybrid is nearly as frost-resistant as the Timberline parent, but the inflorescences are more tender.

The F_2 progeny vary beyond the parental limits, some individuals being consistently more resistant to cold injury than the alpine when observed over a succession of years. Other F_2 plants are fully as susceptible to frost as the Oak Grove parent. All classes of intermediates between these extremes are evident, as a grouping of frequencies in classes grading from class 1 (frost-resistant) to class 5 (frost-susceptible) in the F_2 population of 523 plants suggests:

Class	1	2	3	4	5
Frequency	84	168	112	79	80

The above tabulation is based on numerous observations at Timberline made over a period of 9 years late in the summer after the appearance of frosts. Each plant was rated on an arbitrary scale of 5. The Timberline parent was rated between 1 and 2, the Oak Grove parent as 5, and the reciprocal parent F_1 individuals as 1.4 and 2.8.

Although the Oak Grove parent was highly susceptible to frost injury, it apparently contributed something to some of the progeny to increase their resistance to cold. In the F_1 plants the cold resistance approaches that of the sub-

alpine parent, in the F_2's the frequency distribution is weighted in the direction of the frost-resistant classes, but no clear-cut distinction among the five classes could be observed. Yearly variation was observed in the relative ratings among some of the F_2 plants, apparently a difference depending upon the severity of the frosts and the growth stage of the plants. A considerable proportion of the F_2 progeny were consistently either frost-resistant or frost-susceptible, however, so that the relative ratings of individual plants into the various classes are probably dependable. The degree of cold resistance may to some extent depend on the earlier seasonal history of the plant.

Upper Monarch Lake × Santa Barbara. In the Stanford garden the leaves of the coastal Santa Barbara produced during the late summer and fall are not injured by the frosts occurring during December through February, nor are the new leaves that are normally produced during the winter months. The alpine parent from Upper Monarch Lake, on the other hand, is winter-dormant at Stanford; the old leaves developed during the preceding summer and fall become withered through frost action, and no new growth appears until early in March after most of the danger from frosts is over. In the F_1 hybrid the leaves of the preceding season are frost-killed during the winter, as in the alpine parent, but new growth developing during the winter months is able to resist cold damage, as in the Santa Barbara parent.

Among the F_2 progeny grown at Stanford there was wide segregation with respect to the degree of winter activity and frost damage. In winter-active individuals the new winter leaves were always resistant to the frosts occurring at Stanford, but the leaves produced during the late summer and fall of the preceding growing season were, in some individuals, killed by winter frosts, as in the alpine parent, and in other individuals were resistant to cold, as in Santa Barbara. These facts suggest that frost resistance is governed by genes distinct from genes governing the degree of winter activity, but the two characteristics are closely interrelated.

In view of the complex nature of frost susceptibility, attempts to estimate the minimum number of genes governing the character do not seem to be justified. The main conclusion is that the degree of susceptibility to frost is gene-controlled, and that the control probably is complex. Moreover, in its F_2 segregation, frost susceptibility was found to be correlated with gene-controlled morphological characters, as will be shown in later paragraphs.

19. Earliness of Flowering

Contrasting climatic races usually differ in their time of flowering. If a race is to reproduce itself, its period of flowering and fruiting must fit the seasons in the climate where it is native. The mode of inheritance governing this character is, therefore, of special evolutionary significance.

The study of inheritance governing time of flowering is complicated by the profound modifications induced by environment. When ramets of the same

clone of *Potentilla glandulosa* are grown at the three altitudes of Stanford, Mather, and Timberline, they flower approximately 2 months apart at the successive altitudes. One can, however, compare the flowering sequences of the parental races, their F_1 hybrids, and their F_2 progeny in each environment separately.

Upper Monarch Lake × *Santa Barbara.* In seasonal periodicity the alpine race from Upper Monarch Lake differs greatly from that of Santa Barbara. Nevertheless, when the two races grow together in the same environment at Stanford they happen to flower at nearly the same time. Santa Barbara is winter-active, its growth beginning in the late fall, and an extensive growth of rosette leaves precedes the development of flowers. Upper Monarch Lake, however, which is winter-dormant, flowers almost immediately after breaking dormancy. The result is that the coastal race has a mean flowering date of April 5, 5 days earlier than the date of the alpine parent, April 10. The F_1 was intermediate in earliness, flowering April 8.

In the F_2 the range between the earliest- and the latest-flowering plants extended from March 11 to May 19, a period of 69 days, far transcending the differences between the parents. According to the month during which first flowers appeared, the 992 F_2 progeny were grouped into three broad classes, and their frequency distribution, compared with the earliness of the parents and the F_1, is shown below:

Date of First Flowers

Parents: Santa Barbara, April 5; Upper Monarch Lake, April 10.
F_1: April 8.
F_2 progeny: 243 in March; 650 in April; 79 in May. Total: 992.

The spread between the earliest and latest plants of the F_2 population grown at Stanford was 14 times as great as the spread between the parents, and indicates profound genetic differences between the parents controlling the physiological mechanisms that determine flowering dates. Furthermore, the importance of the interaction between genetic and environmental factors is shown by the fact that at Mather the sequence of the flowering dates in the parents is reversed, Santa Barbara being 3 weeks later than Upper Monarch Lake.

It seems probable that in the parental races independent sets of genes determine the dates of flowering. If we assume that one parent possesses two or three pairs of genes for earliness, and the other two or three other pairs that govern the same character, the F_1 would be expected to have essentially the same earliness as the parents. By recombination many grades of early and late progeny would arise in the F_2. From the above tabulation it is evident that approximately one-fourth of the progeny were earlier than the earliest parent, and this fraction included plants that were taller than either parent. Even more F_2 plants were later in flowering than the Timberline parent. Genes having complementary and inhibiting effects are probably active in addition to the primary genes governing earliness.

Timberline × Oak Grove. In the F_1 and F_2 progenies of the cross Timberline × Oak Grove there is likewise strong environmental modification in the expression of the genotypes. The data from this cross, however, are more complete, because they are based on mean flowering dates of each F_2 clone over a period of 4 years at each station.

At Stanford the mean flowering date of the subalpine Timberline parent is April 8, about a month after it has broken dormancy. The Oak Grove parent flowers approximately a week later, April 15, but only after active new growth

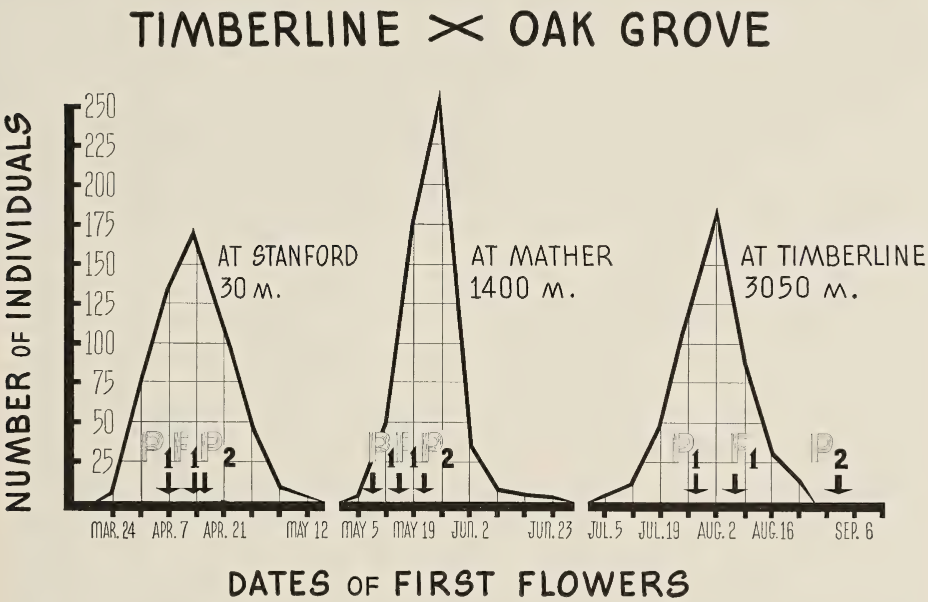

FIG. 22. Frequency diagrams showing average dates of first flowering among 511 F_2 progeny of Timberline × Oak Grove cloned and grown at the Stanford, Mather, and Timberline stations.

Note the shifts in extent and direction of transgression as compared with the parents at the three contrasting environments.

of the leaves has been under way for nearly 2 months. During the years of the experiment the mean date of flowering of the two F_1 parental individuals was April 14. As in the last cross, the parents of the present combination were among the earliest of their races.

The F_2 progeny varied in earliness over a range of 53 days, a spread approximately 7 times as great as that between the parents. The left graph of figure 22 shows the frequency distribution in dates of first flowers in 511 F_2 plants at Stanford as compared with corresponding dates for the parents and the F_1. The extensive transgressive segregation, as in the cross Upper Monarch Lake × Santa Barbara, suggests something of the complexity of the inheritance of genes governing earliness of flowering.

At each station the F_2 population as a whole shows approximately the same spread in time between the earliest and the latest individuals. Flowering dates at Mather are approximately 2 months later than at Stanford, and at Timberline 2 months later than at Mather. This sequence is shown clearly by the frequency curves in figure 22, which also indicate graphically that at each station there is transgressive segregation as measured by the spread between the dates of flowering of the parents and the position of the F_1 hybrids.

At Stanford the segregation is transgressive on both the plus and minus side, whereas at Mather the frequencies are in favor of late-flowering plants. Contrariwise, at Timberline the same cloned F_2 individuals show a marked transgression toward earliness, and none are as late as the Oak Grove parent. These shifts in position at the three stations of the cloned F_2 progeny in relation to the parents demonstrate the complexity of the segregating genotypes as they are expressed in the contrasting environments. The complexity is even greater than is indicated by the graphs, for F_2 individuals that are consistently early at one station may be either early, intermediate, or late at another station, as is described more fully in the next chapter.

The F_3's, grown at Stanford only, were found to show almost as wide a range of segregation within each progeny as the F_2 with respect to flowering dates. Compared with the wide segregation within progenies, the differences in earliness between progenies were relatively small. It would require many generations of selection to obtain populations having a degree of homogeneity in earliness comparable with that of natural populations of *Potentilla glandulosa*.

The available evidence on the inheritance of earliness in contrasting climatic races leaves much to be desired. The principal conclusions that appear to be justified are (1) that differences in earliness are controlled by rather complex systems of genes; (2) that genes for earliness are expressed through processes that are profoundly affected by the environment; (3) that segregation in F_2 progenies far transcends the spread between the parents, and that the segregation continues unabated in F_3 progeny; (4) that the contrasting parental individuals have introduced distinct sets of genes governing flowering time; and (5) that distinct sets of genes probably become activated in different environments.

The facts suggest that earliness of flowering may be controlled by a larger number of genes than any of the other characters that have thus far been discussed.

Minimum Number of Genes Regulating Differences between Races of Potentilla

The preceding study reveals that characters distinguishing climatic races of *Potentilla glandulosa* are governed by intricately balanced gene systems. The inheritance not only of morphological characters, but also of physiological differences such as time of flowering, susceptibility to frost, and growth as expressed in length of stems, is regulated by such systems. There is also evidence

that, in distinct environments, different sets of genes may become activated and influence the expression of the same character, especially physiological characters.

The complex nature of the observed segregation in the F_2 and F_3 progenies of crosses between contrasting climatic races leads us to conclude that the

TABLE 38

ESTIMATE OF MINIMUM NUMBER OF GENES GOVERNING THE INHERITANCE OF 19 CHARACTERS IN TWO INTERECOTYPIC HYBRIDS OF POTENTILLA GLANDULOSA

Character, and action of genes	Estimated no. of gene pairs
1. *Orientation of petals:* 2 erecting, 1 reflexing	3
2. *Petal notch:* 1 producing notch, 2 inhibiting	3
3. *Petal color:* 2 whitening, 2 producing yellow, 1 bleaching	5
4. *Petal width:* 4 widening, 1 complementary, 1 narrowing	6
5. *Petal length:* 4 multiples	*ca.* 4 (plus possible inhibitors)
6. *Sepal length:* 3 or 4 multiples for lengthening, 1 for shortening, 1 complementary	*ca.* 5
7. *Akene weight:* 5 multiples for increasing, 1 for decreasing	*ca.* 6
8. *Akene color:* 4 multiples of equal effect	4
9. *Branching, angle of*	*ca.* 2 (also genes for strict to flexuous branching)
10. *Inflorescence, density of*	*ca.* 1 (plus modifiers)
11. *Crown height*	*ca.* 3 (also genes for presence or absence of rhizomes and for thickness of rhizomes, to which crown height is related)
12. *Anthocyanin:* 4 multiples (1 expressed only at Timberline), 1 complementary	5
13. *Glandular pubescence:* 5 multiples, in series of decreasing strength	5
14. *Leaf length:* transgressive segregation; many patterns of expression in contrasting environments; possibly different sets of multiples activated	*ca.* 10–20
15. *Leaflet number in bracts*	*ca.* 1 (plus modifiers)
16. *Stem length:* transgressive segregation, 5 to 6 multiples plus inhibitory and complementary genes; many patterns of expression in contrasting environments	*ca.* 10–20
17. *Winter dormancy:* 3 multiples of equal effect	3
18. *Frost susceptibility:* slight transgression toward resistance	*ca.* 4
19. *Earliness of flowering:* strongly transgressive; many patterns of altitudinal expression; possibly different sets of genes activated	many

genetic systems that regulate individual characters consist of multiple or polymeric genes, some of which are positive, enhancing the expression of a character, and others negative, inhibiting expression in various degrees. Complementary genes that activate specific genes in a multiple series also play a part in such systems.

An attempt has been made in table 38 to summarize the results of this inquiry

by indicating the kind and number of genes that regulate the expression of the various characters of contrasting ecological races of a diploid species such as *Potentilla glandulosa.* In view of the complex nature of the gene systems, it is obvious that any estimate must be highly tentative. On the basis of the inheritance of the 19 characters reviewed in the preceding pages, however, it is possible to acquire an over-all picture of the gene systems. For some of the characters listed, the estimate of the genes in operation is considered by the authors to be reasonably accurate; for other characters the number of genes can only be conjectured from systems that have been analyzed. Values in the table that are preceded by the designation *ca.* are tentative only.

If such physiologically controlled characters as stem length and earliness of flowering were to be studied through F_3 and even F_4 progenies as cloned transplants in three or more environments, it might be possible to trace the number and kind of genes active in each environment. Such a study would probably disclose that the number of genes regulating each character is higher than is indicated in our present estimate.

The total of the estimated minimum number of pairs of genes that regulate the expressions of the first 18 characters listed in table 38 is about 80, and for all 19 it is possibly about 100 or more. Considered in terms of the complex array of observed recombinations that can be accounted for in the F_2 and F_3 combinations, this number seems to be remarkably small. Thus with a rather limited number of basic genetic building blocks the diploid species *Potentilla glandulosa* apparently has been able to evolve an extensive array of ecological races fitted to diverse environments.

Although our estimate is a bare minimum based on a limited number of characters, the important fact emerges that the genetic systems governing the inheritance of ecological races are by no means infinitely complex. The inquiry indicates that the differences can be resolved in terms of a reasonable number of genes that is well within the range of experimental study.

GENETIC CORRELATION

In view of the many genes that have been found to regulate characters that distinguish ecological races, the question arises whether there is evidence of genetic linkage among the offspring of segregating second-generation hybrids. *Potentilla glandulosa* has only 7 pairs of chromosomes; therefore, because a minimum of approximately 100 pairs of genes govern the 19 characters investigated, one would expect for these characters an average of 14 genes per chromosome. In such a situation a considerable degree of genetic linkage would be expected.

The determination of the degree of correlation between segregating characters of an F_2 progeny is one step in ascertaining whether or not genetic linkage occurs. Because the gene systems of ecological races of *Potentilla* may contain both oppositional and complementary components, the degrees of correlation,

or the absences of correlation, that are observed may not be a direct measure of actual genetic linkage.

An observed correlation between two segregating characters in the F_2 is a correlation between the resultant effects of all the genes that regulate these characters, and does not necessarily indicate linkage between individual genes. Fortunately, the overwhelming majority of genes governing characters in *Potentilla* races were of the multiple kind having a positive effect, so that it was possible to trace the parental origin of the individual genes. In these circumstances, correlation may serve as an indicator of genetic linkage.

Systems containing oppositional or complementary genes are especially deceptive in linkage studies. An increase in size, for example, may be caused either by a gene having a positive effect or by the recessive allele of an inhibitor or suppressor. Characters that show excessive transgressive segregation are also poor indicators of genetic linkage because it is impossible to determine from which parent any particular gene came. An example is date of flowering, discussed on pages 105 to 108.

METHOD USED IN DETERMINING GENETIC CORRELATION. The determination of correlation was greatly facilitated by the use of punched cards, as described on pages 32 to 35. In the cross Upper Monarch Lake × Santa Barbara, for example, in which 14 characters were studied, it was possible to determine systematically the correlation coefficient in all the 91 character combinations that are possible when 14 characters are grouped into pairs.

Code numbers punched on the cards of each plant for each character indicate the class value or the approximate grade of expression of that character. The punched code numbers make it possible to select by machine the cards of plants having specified class values for two characters. The number of plants having the required characteristics were then recorded as frequencies and used in computing the value of the correlation coefficient r.

The values of r were computed with the aid of calculating machines according to the standard formula as used by Fisher (1936) and Snedecor (1937, p. 118):

$$r = \frac{Sf(x \cdot y)}{\sqrt{Sfx^2 \cdot Sfy^2}}.$$

In this formula, r is the correlation coefficient, x and y are the mean class values of the two characters being compared, f is the frequency of each class, and S is the summation of the values indicated.

Another formula which is more applicable to calculating-machine computation and which gives the same result is the following:

$$r = \frac{N \cdot Sf(X \cdot Y) - SfX \cdot SfY}{\sqrt{(N \cdot SfX^2 - SfX^2) \cdot (N \cdot SfY^2 - SfY^2)}}.$$

In this formula X and Y represent the class values of the two characters being compared, f the frequencies in each class, S their sums, and N the total number of individuals classified.

The correlation coefficient, r, is a test of correlation. By implication it may be regarded as a quantitative estimate of the degree to which two characters are correlated, or as a measure of randomness of segregation among F_2 individuals. The more closely the value of r approaches zero, the more nearly can the segregation be regarded as a random one. On the other hand, the more closely this value approaches ± 1, the more completely are the characters linked by some genetic mechanism.

In the present study the value of r measures approximately the correlation between gradations in the expression of two characters that are determined by complex gene systems. It does not measure the degree of linkage between individual genes that determine the phenotypes. Far more detailed data from segregating F_3's, F_4's, and even later generations would be necessary in order to compute the actual linkages among individual genes of systems as complicated as those regulating the differences among climatic races of *Potentilla glandulosa*.

Through the use of tables computed by Fisher on the basis of the null hypothesis (Snedecor, 1937, p. 125) an estimate can be made, for a sample of any given size, of the degree of significance to be attached to any particular value of r. In the cross Upper Monarch Lake × Santa Barbara, for example, the F_2 sample consists of approximately 1000 plants; in a population of this size, values of r above 0.062 are considered to be significant at the 5 per cent level, and those above 0.081 are considered to be significant at the 1 per cent level. In this cross only the more strict test of r at the 1 per cent level of 0.081 or higher was regarded as indicating a significant degree of correlation. Values below this figure were considered to indicate random segregation.

In the cross Timberline × Oak Grove the segregations of individual characters were determined on samples of approximately 500 F_2 plants. In a sample of this size an r value of 0.088 is considered to be significant at the 5 per cent level, and one of 0.115 to be significant at the 1 per cent level. The r values in this cross tend to fall either below the 5 per cent level of significance or above the 1 per cent level. Since only two character pairs had an intermediate r value just below the 1 per cent level, the 5 per cent value was used as a more logical measure of correlation.

Results of correlation studies. The genetic significance of correlations and the difficulty in applying them directly in estimating linkage of individual genes are most easily seen through examples.

The correlation between petal orientation and petal color among the F_2 progeny of the cross Timberline × Oak Grove, for example, represents a relatively simple case. The F_2 plants were rated into 5 classes according to petal color, and into 2 classes in relation to petal orientation, thus providing 10 combinations. The frequencies in the 10 combinations are listed in table 39, from

which it is fairly evident by inspection that plants with reflexed petals and yellow and cream-yellow petals occur more frequently than plants with reflexed petals that are white. The correlation coefficient is 0.213, which, considering the size of the population, is clearly significant, and so high as to exclude a probability of purely random recombination.

Three pairs of genes appear to determine the inheritance of petal orientation (table 14, p. 55), and approximately five regulate petal color (table 18, p. 64). Reflexed petals are realized only in the presence of the reflexing gene, R, and in the absence of both the genes for erect petals, E_1 and E_2. Likewise, deep yellow petals are expressed only in the presence of gene Y_1, and in the absence of both

TABLE 39

CORRELATION BETWEEN COLOR AND PETAL ORIENTATION IN F_2 PROGENY OF TIMBERLINE × OAK GROVE AS SHOWN BY FREQUENCY DISTRIBUTIONS. CORRELATION COEFFICIENT = 0.213.

Petal orientation, classes	Petal color, classes					Totals	
	1 White	2 Cream-white	3 Cream	4 Cream-yellow	5 Yellow	Observed	Calculated
1. Horizontal-upcurved	70	85	202	151	39	547	549.0
2. Reflexed	..	1	4	11	10	26	27.0
Totals							
observed	70	86	206	162	49	573	573.0
calculated	58.2	67.7	219.6	182.7	44.8	573.0	

Gametic formulas

Timberline: E_1E_2r; $W_1W_2y_1Y_2B$
Oak Grove: e_1e_2R; $w_1w_2Y_1y_2b$

Linked genes

$$\frac{r\ y_1}{R\ Y_1}$$

whitening genes, W_1 and W_2. Both the R and Y_1 genes were introduced into the hybrid through the Oak Grove *reflexa* parent, whereas the alternate recessive genes, r and y_1, originated from the Timberline *nevadensis* parent. Apparently these two pairs of genes are located in the same pair of chromosomes. The strongest evidence for genetic linkage between Y_1 and R is the frequent association of yellow color with reflexed petals. This conclusion is confirmed by the reciprocal association of characters in which the frequency of plants having white, horizontal to upcurved petals is compared with the number of plants having white, reflexed petals. Among 70 white-petaled F_2 plants, none had reflexed petals, whereas by free recombination 3 individuals with this combination of characters would be expected.

A more complex example of genetic linkage is found in the correlation between petal color and petal size in the F_2 of Timberline × Oak Grove, as indi-

cated in table 40. The correlation between large size of petals and white color as compared with small size of petals and yellow color is obvious from inspection of the table. There are 5 classes in petal size, the subalpine parent, which has the largest petals, being represented by class 1. There are also 5 degrees in petal color, starting with the subalpine white and ranging to the deep yellow of *reflexa,* therefore 25 combinations of classes are provided to test against one another for correlation. The correlation between large and white versus small and yellow petals is high, the value of r being 0.565, and it is in the same direction as that in which the characters were introduced by the parents. There is little doubt that this correlation indicates a fairly strong genetic linkage, but it is impossible with the present data to pinpoint the linkage to individual genes.

TABLE 40

CORRELATION BETWEEN PETAL COLOR AND PETAL LENGTH IN F_2 PROGENY OF TIMBERLINE × OAK GROVE. CORRELATION COEFFICIENT = 0.565.

PETAL LENGTH, CLASSES	PETAL COLOR, CLASSES					TOTALS
	1 White	2 Cream-white	3 Cream	4 Cream-yellow	5 Yellow	
1. Longer than sepals	65	54	125	32	1	277
2. Long to intermediate	1	25	46	38	5	115
3. Intermediate (equal to sepals)	2	4	21	53	13	93
4. Intermediate to short	. .	3	8	23	12	46
5. Shorter than sepals	1	. .	6	16	18	41
Totals	69	86	206	162	49	572

With respect to petal size, the segregation listed in table 24, page 74, suggests that one fairly dominant gene, which may be designated Pl_1, is primarily responsible for the large petals of the Timberline plant. With respect to petal color, however, the F_2 plants are white because of the absence of the Y_1 gene for deep yellow petals, symbolized by y_1, and because of the presence of either of two W_1 and W_2 genes for white petals, all carried by the Timberline parent (table 18, p. 64). It is not possible from information now available to determine which of these three color genes from the Timberline parent are linked to the Pl_1 gene for large petals. There is some indication that two color genes of the Timberline parent, W_2 and y_1, are linked; it is possible that the primary gene for large petals, Pl_1, may also belong to this linkage group, so that the genes r, W_2, y_1, and Pl_1 may all be carried in one pair of chromosomes.

UPPER MONARCH LAKE × SANTA BARBARA. The correlation coefficients, r, for all 91 possible combinations of character pairs for F_2 progeny of the cross Upper Monarch Lake × Santa Barbara have been determined and are summarized in the graph shown in figure 23. Values of r higher than those significant at the

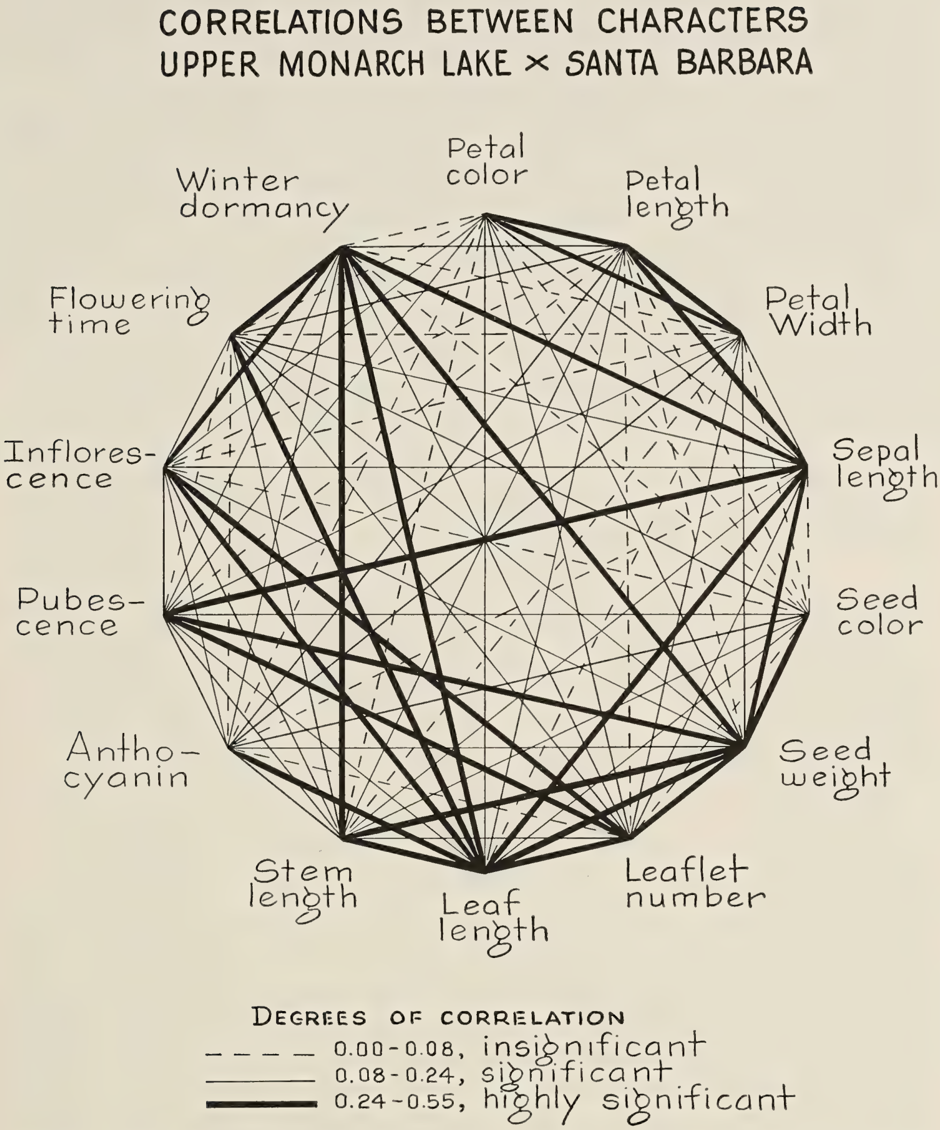

FIG. 23. Graph summarizing statistical correlations between pairs of characters as expressed in approximately 992 F_2 progeny of Upper Monarch Lake × Santa Barbara grown at Stanford.

Values of the correlation coefficient r above the 1 per cent level (0.08) are considered to be significant. Note the relatively large number of character pairs that show significant partial correlations.

1 per cent level are considered to indicate some degree of genetic linkage and are shown by solid lines; those less than this value are regarded as insignificant and are shown as broken lines. Pairs of characters having values of *r* of 0.24 or greater are rated as highly significant and are shown by the heavy lines.

It is of considerable significance to determine whether the pairs of characters are correlated in the same direction in which they entered the hybrid from the parental races, or in an opposite direction. All 91 segregating combinations of character pairs in the F_2 of Upper Monarch Lake × Santa Barbara are classified in table 41 with regard to their degrees of correlation, and to the direction in which the correlations occurred. Among the 67 pairs of characters showing a

TABLE 41

FREQUENCY OF VARIOUS DEGREES OF CORRELATION BETWEEN SEGREGATING CHARACTERS OF F_2 PROGENY OF UPPER MONARCH LAKE × SANTA BARBARA

VALUES OF *r*	CORRELATION INSIGNIFICANT	CORRELATION SIGNIFICANT: In same direction as in parents	CORRELATION SIGNIFICANT: In direction opposite that in parents
0.00–0.09	24	..	..
0.09–0.20	..	25	3
0.20–0.30	..	21	2
0.30–0.40	..	11	1
0.40–0.50	..	1	..
0.50–0.60	..	2	..
0.60–0.70	..	0	..
0.70–0.80	..	1	..
0.80–0.90	..	0	..
0.90–1.00	..	0	..
Totals	24	61	6

statistically significant correlation, 61 are in the same direction as in the parental races, and only 6 in the opposite direction. Five of the latter category included combinations involving petal length, in which long sepals are linked with long petals, long petals with long leaves, and long petals with long stems. The fact that the great preponderance of correlations are clearly in the same direction as in the parents shows an over-all coherence among the parental characters, and this finding has a definite bearing on the genetic interpretation of taxonomically differentiated subspecific groups.

TIMBERLINE × OAK GROVE. The general pattern of linkage between the possible combinations of character pairs of Timberline × Oak Grove is similar to that in Upper Monarch Lake × Santa Barbara. The *r* values of 66 pairs of character combinations are listed in table 42. Thirty-eight of these show a statisti-

cally significant correlation at the 5 per cent level, whereas 28 do not. Among those showing correlation, only 5 are in a direction opposite to that shown by the parents, and 32 are in the same direction.

Figure 24 summarizes in graphic form the data listed in table 42 and can be compared with the preceding figure showing the degrees of correlation in Upper Monarch Lake × Santa Barbara. The degrees of coherence between characters are relatively similar in both crosses, but it is evident from the diagrams that they are not identical. The more highly significant correlations appear to be less numerous in Timberline × Oak Grove than in Upper Monarch Lake × Santa Barbara, but the sets of characters studied in the two crosses are not the same and therefore are not strictly comparable. It will be recalled that in the cross Timberline × Oak Grove it was the Mather expressions of leaf length, stem length (height), and date of first flowers that were used for the calculation of correlations rather than the corresponding Stanford data, as in the cross of Upper Monarch Lake × Santa Barbara.

In both hybrids there are significant partial correlations between independent characters that distinguish the subspecies. These correlations provide a loose bond that may be one of the genetic bases for taxonomic entities.

Effects of certain genetic systems on correlation between characters. A complication arises when two characters show correlation opposite to the parental combinations. In table 43 are listed the relatively few instances of pairs of characters showing such negative correlations in the crosses Upper Monarch Lake × Santa Barbara and Timberline × Oak Grove. Examples of this kind would be expected to occur when one or both of the character pairs is controlled by complementary or oppositional genes.

Six of the negative correlations in table 43 involve petal length. In both crossings petal length appears to be governed by a system containing at least one shortening in addition to several lengthening genes. There is reason to believe that the shortening gene may be linked with genes for the other correlated characters, and that this gene is carried by the long-petaled parent together with several additive lengthening genes. Under such circumstances the linkage of the shortening gene would result in a negative correlation with respect to petal length.

Petal width shows negative correlations with three other characters. The inheritance of petal width is in part governed by two pairs of genes that are complementary, so that one activates the other (p. 70). In two of the three instances listed in table 43, the activating complementary gene was carried by the narrow-petaled parent, but could not be expressed unless complemented by a gene inducing wide petals from the other parent which, by itself, is inactive. The narrow-petaled parent therefore contributes to the widening of the petals in the hybrid progeny, and the linkage of this gene results in a negative correlation in the segregating F_2.

TABLE 42

Correlation coefficients between pairs of characters among segregating F_2 progeny of Timberline × Oak Grove

Character pairs and range of expression from Timberline to Oak Grove		Correlation	
		Significant	Insignificant
Petal orientation: ascending to reflexed	Petal width: wide to narrow	+0.289	......
	Petal notch: notched to entire	+0.126	......
	Petal length: long to short	+0.201	......
	Petal color: white to yellow	+0.213	......
	Crown height: 0 to 13 cm.	+0.189	......
	Branching: erect to divaricate	......	+0.039
	Anthocyanin: green to red	......	+0.018
	Frost susceptibility: resistant to susceptible	......	+0.080
	First flowers: early to late	......	—0.017
	Leaf length: short to long	......	+0.063
	Stem height: short to tall	......	+0.070
Petal width: wide to narrow	Petal notch: notched to entire	+0.106	......
	Petal length: long to short	+0.102	......
	Petal color: white to yellow	+0.169	......
	Crown height: 0 to 13 cm.	......	—0.049
	Branching: erect to divaricate	—0.104*	......
	Anthocyanin: green to red	—0.126*	......
	Frost susceptibility: resistant to susceptible	......	+0.043
	First flowers: early to late	+0.120	......
	Leaf length: short to long	......	+0.013
	Height: short to tall	—0.088	......

* Characters correlated in a direction opposite to that of their occurrence in the parents.

(*Continued on following page*)

TABLE 42—*Continued*

Character pairs and range of expression from Timberline to Oak Grove		Correlation	
		Significant	Insignificant
Petal notch: notched to entire	Petal length: long to short	......	+0.059
	Petal color: white to yellow	+0.153	......
	Crown height: 0 to 13 cm.	+0.187	......
	Branching: erect to divaricate	+0.132	......
	Anthocyanin: green to red	......	—0.005
	Frost susceptibility: resistant to susceptible	+0.251	......
	First flowers: early to late	......	—0.010
	Leaf length: short to long	......	—0.018
	Height: short to tall	......	+0.076
Petal length: long to short	Petal color: white to yellow	+0.565	......
	Crown height: 0 to 13 cm.	+0.092	......
	Branching: erect to divaricate	......	—0.081
	Anthocyanin: green to red	......	+0.002
	Frost susceptibility: resistant to susceptible	+0.107	......
	First flowers: early to late	......	+0.059
	Leaf length: short to long	......	—0.001
	Height: short to tall	—0.185*	......
Petal color: white to yellow	Crown height: 0 to 13 cm.	+0.194	......
	Branching: erect to divaricate	......	+0.069
	Anthocyanin: green to red	......	—0.054
	Frost susceptibility: resistant to susceptible	+0.123	......
	First flowers: early to late	......	+0.046
	Leaf length: short to long	+0.263	......
	Height: short to tall	......	+0.014

* Characters correlated in a direction opposite to that of their occurrence in the parents.

(*Continued on following page*)

TABLE 42—*Continued*

Character pairs and range of expression from Timberline to Oak Grove		Correlation	
		Significant	Insignificant
Crown height: 0 to 13 cm.	Branching: erect to divaricatae	+0.317	......
	Anthocyanin: green to red	+0.159	......
	Frost susceptibility: resistant to susceptible	+0.186	......
	First flowers: early to late	......	+0.024
	Leaf length: short to long	+0.287	......
	Height: short to tall	+0.311	......
Branching: erect to divaricate	Anthocyanin: green to red	+0.319	......
	Frost susceptibility: resistant to susceptible	+0.195	......
	First flowers: early to late	......	+0.043
	Leaf length: short to long	+0.306	......
	Height: short to tall	+0.417	......
Anthocyanin: green to red	Frost susceptibility: resistant to susceptible	+0.167	......
	First flowers: early to late	......	+0.068
	Leaf length: short to long	......	+0.068
	Height: short to tall	+0.242	......
Frost susceptibility: resistant to susceptible	First flowers: early to late	—0.354	......
	Leaf length: short to long	......	+0.007
	Height: short to tall	......	—0.012
First flowers: early to late	Leaf length: short to long	—0.223*	......
	Height: short to tall	—0.109*	......
Leaf length: short to long	Height: short to tall	+0.638	......

* Characters correlated in a direction opposite to that of their occurrence in the parents.

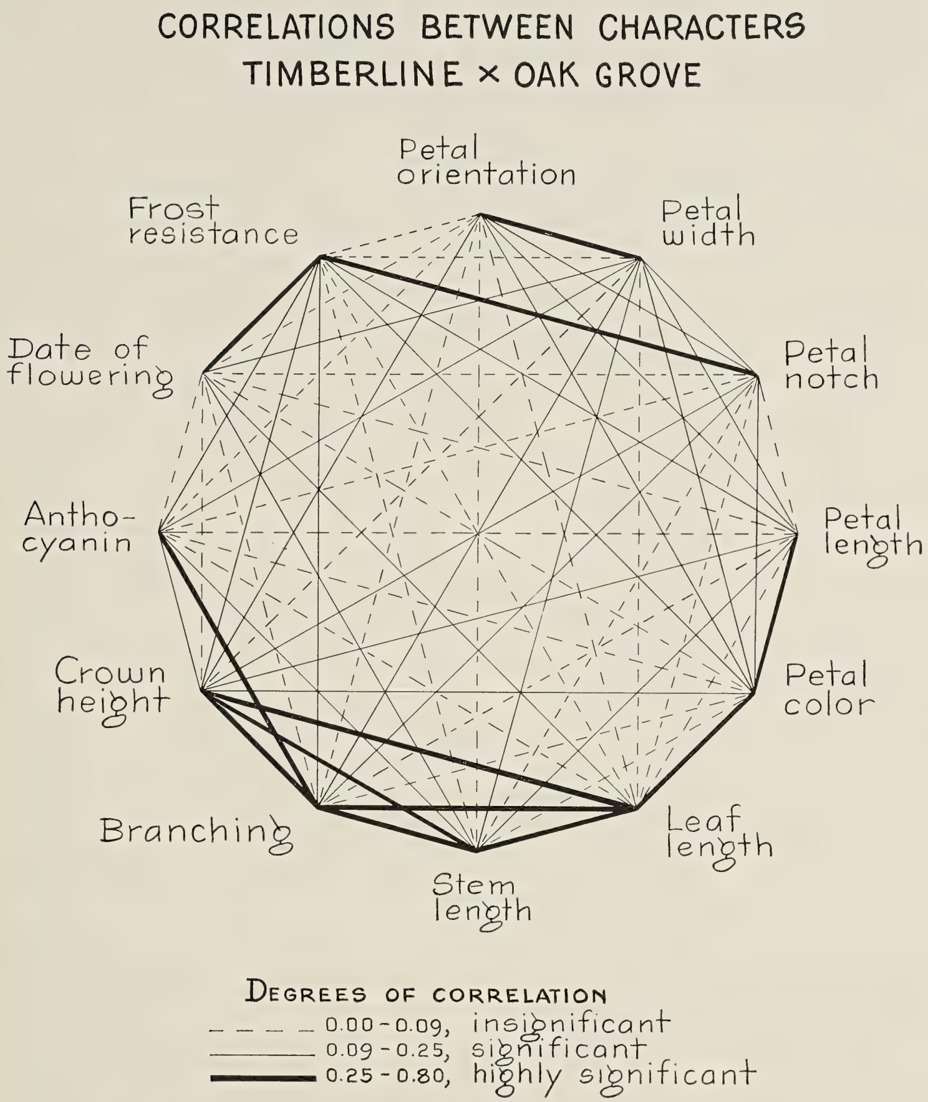

FIG. 24. Graph indicating statistical correlations between pairs of characters in approximately 570 F_2 progeny of Timberline × Oak Grove.

Values of the correlation coefficient r above the 5 per cent level (0.09) are considered to be significant. See table 42 for a complete listing of the r values.

There are also probably undetected linkages. In cases where each of two pairs of characters is controlled by at least one gene having a positive and another having a negative effect, the possibility exists that two linkages may occur, one between positive and the other between negative genes. These would tend to cancel each other, or, if the two linkages are not equally close, their effects would

TABLE 43

CORRELATIONS OPPOSITE IN DIRECTION TO THE CHARACTER ASSOCIATIONS IN THE PARENTS

Character pairs		Cross	Correlation coefficient
Petal length: long to short	Winter dormancy: dormant to active	Upper M. Lake × S. Barbara	—0.135
	Anthocyanin: green to dark	Upper M. Lake × S. Barbara	—0.104
	Leaf length: short to long	Upper M. Lake × S. Barbara	—0.207
	Stem height: short to tall	Upper M. Lake × S. Barbara	—0.200
	Sepal length: short to long	Upper M. Lake × S. Barbara	—0.347
	Stem height: short to tall	Timberline × Oak Grove	—0.185
Petal width: wide to narrow	Anthocyanin: green to dark	Upper M. Lake × S. Barbara	—0.183
	Anthocyanin: green to dark	Timberline × Oak Grove	—0.126
	Branching: erect to divaricate	Timberline × Oak Grove	—0.104
First flowers: early to late	Leaf length: short to long	Timberline × Oak Grove	—0.223
	Stem height: short to tall	Timberline × Oak Grove	—0.109

be expressed as a reduced correlation, positive or negative, depending upon the relative strength of the two linkages.

In examples like those mentioned above where systems of genes other than the simple additive type exist, or where the parental origin of the linked genes cannot be determined, the observed correlations do not truly represent the existence of, or degree of, genetic linkage. It is to be expected that the actual genetic linkages are more frequent and closer than the observed correlations indicate.

III

RESPONSE PATTERNS AT CONTRASTING ALTITUDES

Basic to an understanding of genetics, and of the processes of natural selection, is knowledge concerning the phenotypic expression of genes and of gene combinations over a range of environments. This aspect of genetics has been explored but little. The responses of clones of the highly segregating F_2 progeny of the cross Timberline × Oak Grove, when subjected to the environments at Stanford, Mather, and Timberline, provide data bearing on these matters. The present chapter will be devoted to a review of these data.

The individual F_2 plants show extreme diversity in their growth responses at the three transplant stations over a period of years. Examples are shown in figures 25 to 30, which illustrate the responses of the parents, the reciprocal F_1 hybrids, and sample F_2 progeny. The illustrations are composed of herbarium specimens taken from clones grown at the three stations, and they indicate the approximate over-all effect of transplanting as determined by 5 years' observations at Stanford, and 9 years' at Mather and Timberline.

The subalpine parent, 1113-6, illustrated in figure 25, shows relatively little modification, although it has larger leaves and taller stems, and makes greater growth, at Mather than at either Timberline or Stanford. It is especially reduced in size and vigor at Stanford, where it tends to die after a progressive decline over several years. The foothill parent, 1127-1, differs from the subalpine in its inability to survive at the alpine station, as shown after seven trials, although occasionally it will survive a single winter and develop miniature leaves and a much reduced flowering stem, as shown in figure 25. At Mather it grows with luxuriant vigor and attains its maximum size of stems and leaves, but it also survives well at Stanford for an indefinite period.

The two reciprocal F_1 individuals, 1442-1 and 1443-1 of figure 26, show a wider range of tolerance than either parent, for they are able to survive and grow vigorously at all three transplant stations over a long period of time. They become modified in size and attain their maximum growth at Mather. No significant differences have been observed in the responses of the two reciprocals.

The F_2 progeny transcend the parents in the range of responses found, and no two F_2 individuals respond exactly alike. The kinds of response patterns observed, however, can be roughly exemplified by types, some of which are shown in figures 27 to 30. Individuals representing patterns of contrasting responses at the three stations are paired together in the same figure, except in figure 30.

In figure 27, plant 226 has a record of being consistently vigorous at Timberline, of having only moderate vigor at Mather, and being weak at Stanford, a fact reflected by the modifications in size of the leaves and stems. In the same figure the responses of plant 468 having an opposite growth pattern are illustrated. Both these F_2 individuals are evidently limited in their range of tolerance. Plant 226 is capable of surviving only in an environment approaching

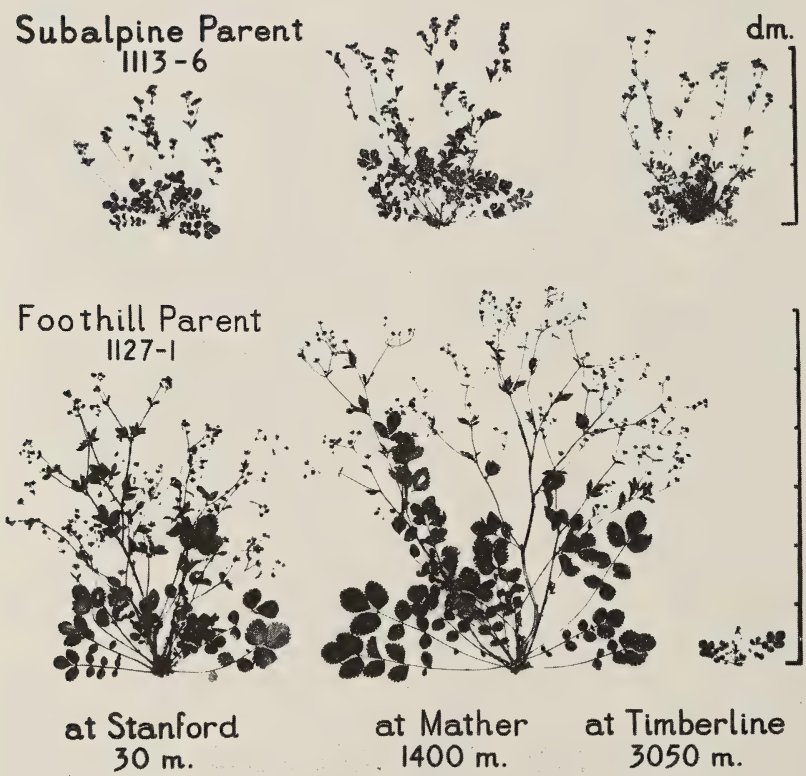

FIG. 25. Modifications in growth of the Timberline (*above*) and Oak Grove (*below*) parents at Stanford, Mather, and Timberline.

The herbarium specimens are from the two parental clones grown at the three transplant stations; they show average responses, except that Oak Grove, the foothill parent, usually dies during the first winter at Timberline.

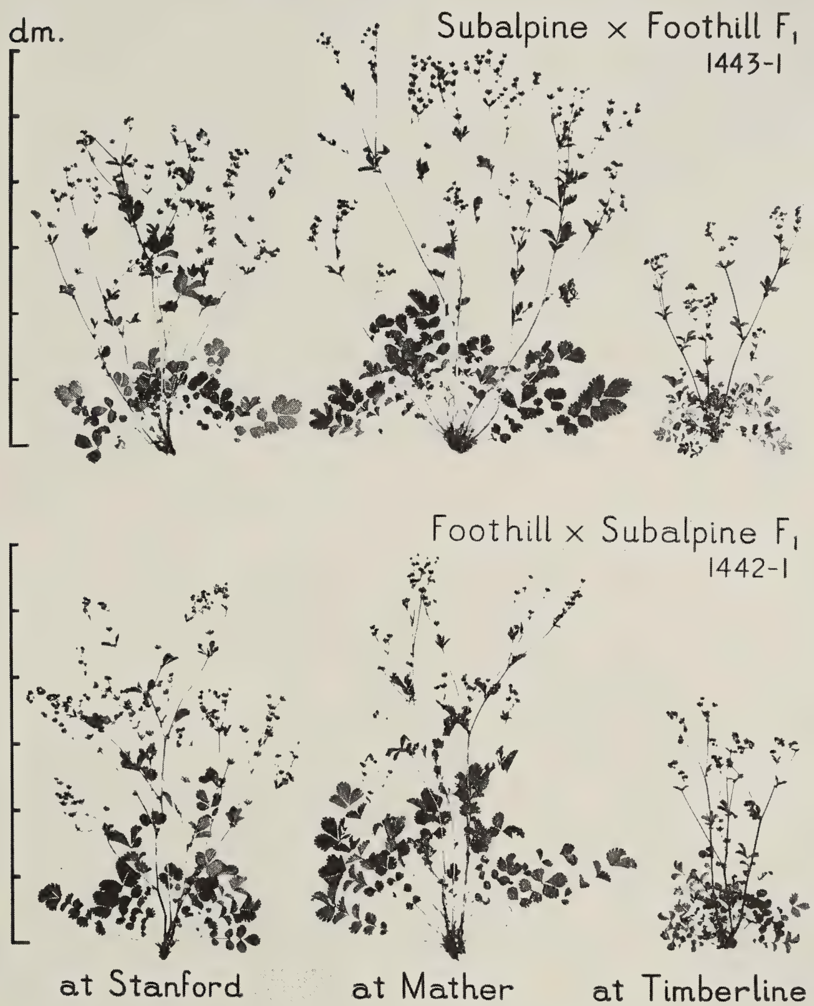

FIG. 26. Modifications in growth of the F_1 hybrid, Timberline × Oak Grove (*above*), and its reciprocal, Oak Grove × Timberline (*below*), at Stanford, Mather, and Timberline. The herbarium specimens are from ramets grown at the three transplant stations and show average responses. Compare with figure 25.

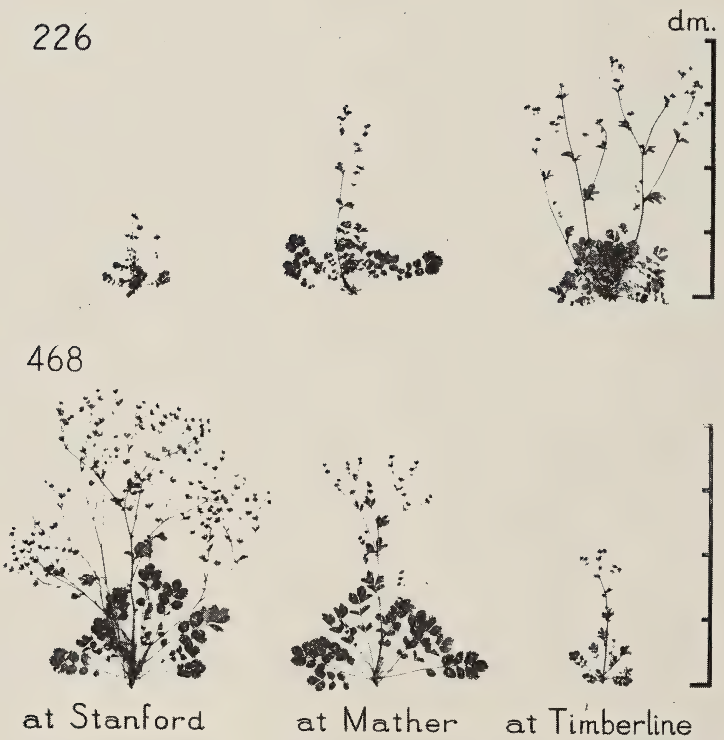

FIG. 27. Modifications in two F_2 individuals of the cross Timberline × Oak Grove, 226 and 468.

Vegetative propagules of each plant were set in gardens at the three stations during the spring and summer of 1938; the herbarium specimens, taken during 1941 and 1942, show typical responses for these individuals.

the Timberline conditions, and plant 468 in climates approaching the one at Stanford.

Wider tolerances are shown by plants 109 and 290, illustrated in figure 28. Both grow well at Mather, but the two differ in that 109 is favored by conditions at Mather and Timberline, whereas 290 grows better at the two lower stations.

Some transplanted F_2 progeny show relatively little modification despite the extreme differences in climate represented at the three transplant stations. Two examples are shown in figure 29. Clone 453 is consistently dwarf and never becomes vigorous in growth at any of the stations, whereas clone 446 is consistently tall and vigorous in all environments. There are some modifications, especially at Timberline, where stems and leaves are reduced in size as compared with those produced at Mather; these minor modifications are most evident on 446, the taller and more vigorous of the two. A point of special interest is the apparent high range of tolerance to all three environments of both of these very different types of progeny, a tolerance that is definitely greater than that of either parent, and similar to that of the F_1 plants shown in figure 26. Clone 453, although low in vigor, has a good survival record at all three stations.

Another type of growth response is exemplified by plant 506, shown in figure 30, in which the greatest vigor is attained at Mather, being much reduced both at Stanford and at Timberline. This pattern is unlike that of either parent, and reflects a more limited range of tolerance than that of the plants illustrated in figure 29. An even more contrasting kind of specialization is represented by 19 F_2 plants which have shorter stems at Mather than at Stanford and Timberline. This group is exemplified by such plants as 174 and 497, listed in table 35, page 98.

These examples serve to illustrate the diversity of growth responses represented among the various classes of F_2 progeny. A more detailed study of the modifications of specific characters, and of the response patterns of genetic characteristics in different environments, will be considered in the pages that follow.

MODIFICATIONS OF CHARACTERS

Not all characters are modified to the same degree in contrasting environments. Among those only moderately influenced by the environment are petal color, petal size, petal notch, and the degree of anthocyanin coloration, characters whose inheritance and modifications were discussed in chapter II. Although such "qualitative" characters are relatively slightly modified from station to station, the influences of contrasting environments are sufficient to change perceptibly the phenotypic expressions of the genotype.

Other characters, commonly referred to as "quantitative," are highly modifiable to the extent that the influence of environment upon their expression may easily overshadow genetic differences. The highly modifiable characters, mostly developmental and relating to growth, include size relations of leaves and stems, total growth as expressed in vigor, and seasonal characteristics such as period of winter dormancy and time of flowering.

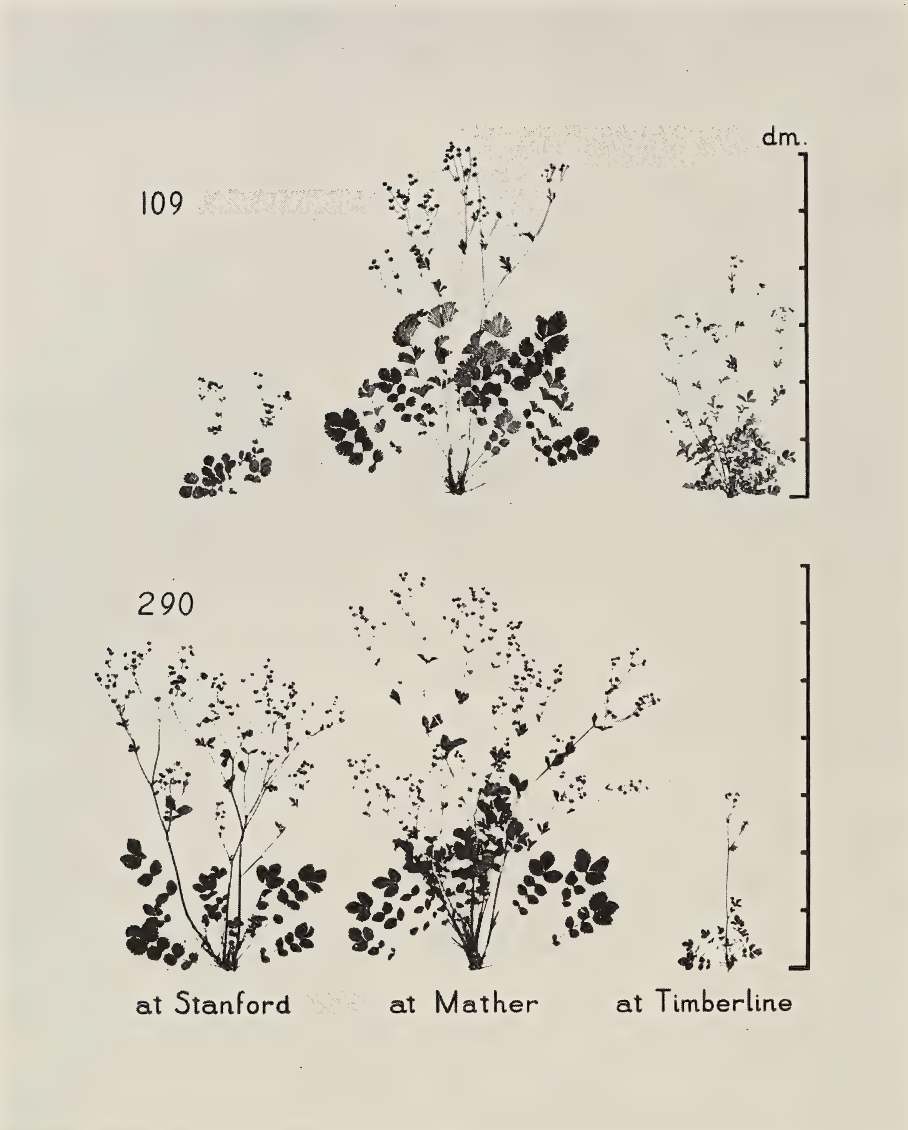

Fig. 28. Modifications in two F_2 individuals of the cross Timberline × Oak Grove, 109 and 290.

Propagules of each plant were set at the three stations during the spring and summer of 1938; typical herbarium specimens were taken during 1941 and 1942.

Fig. 29. Modifications in two F_2 individuals of the cross Timberline × Oak Grove, 453 and 446.

Propagules of each plant were set at the three stations during the spring and summer of 1938; typical herbarium specimens were taken during 1941 and 1942.

Attempts to analyze the genic control of the quantitative characters have not succeeded because the systems that control them are too complex to be interpreted on the basis of the present data. Evidence indicating the genetic complexity of these characters lies chiefly in the transgressive type of segregation observed in the F_2 progeny. Not only does the extent of transgression differ with the environment, but also the direction of the observed transgressions with respect to the parents may differ. The environmental expressions of the highly modifiable characters at the three stations will be discussed below in some detail.

FIG. 30. Modifications in an F_2 individual, 506, of the cross Timberline × Oak Grove. The propagules were set at the three stations during the spring and summer of 1938; the herbarium specimens were taken during 1941 and 1942 and represent typical responses.

1. LEAF LENGTH. Size of leaves is a highly modifiable character closely related to growth. That size of leaves is also controlled genetically is clear from the evidence presented in chapter I, with examples shown in figures 3 and 4. The study of the inheritance of leaf length is strongly confounded by modifications, as mentioned in chapter II and illustrated in figure 19. In the cross Timberline × Oak Grove the F_2 progeny of cloned plants grown at Stanford, Mather, and Timberline appeared as though they belonged to three genetically distinct populations, rather than to an identical population. The relative positions of the parents with respect to the F_2 progeny may be changed or even reversed. Moreover, the relation of each F_2 individual to the population as a whole varies from station to station.

The shifts in relative length of leaves of some of the individual clones at the three stations are listed in terms of classes under the notation LL in table 44. At each station eight classes are recognized, class 1 having the shortest leaves,

TABLE 44

DESCRIPTION OF PARENTS, F_1'S, AND SAMPLE F_2'S OF TIMBERLINE × OAK GROVE IN TERMS OF CLASS VALUES

PLANT NO.	CHARACTERS (SEE FOOTNOTES AND TABLE 12 FOR EXPLANATION OF SYMBOLS AND CLASS VALUES)																	INDEX VALUES
	PO	PW	PN	PL	PC	Cr	Br	An	FR	Vig SMT	RoW SMT	StN SMT	DFF SMT	LL SMT	StL SMT	Sur SMT	SP	
Subalpine parent																		
1113-6	1	1	1	1	1	1	1	1	1	354	246	255	324	235	246	399	2	19
Foothill parent																		
1127-1	2	2	4	5	5	3	3	5	5	561	55–	52–	439	665	562	591	7	53
F_1's																		
1443-1	1	1	2	1	3	..	2	3	2	563	456	442	536	356	555	599	5	33
-2	1	1	2	1	3	2	2	3	2	464	456	442	435	475	456	599	5	34
F_1 reciprocals																		
1442-1	1	1	3	1	3	2	2	3	3	665	557	443	436	445	457	599	5	34
-2	1	1	3	1	3	..	2	3	4	453	336	442	546	577	566	559	5	40
F_2's																		
1*	1	1	1	1	1	2	1	2	1	444	326	223	446	234	345	599	5	25
2*	1	1	2	1	1	2	2	5	5	332	222	221	247	223	443	396	3	31
3	1	1	2	1	1	1	1	2	2	244	235	243	335	143	347	399	2	24
4	1	1	1	1	1	1	1	2	3	444	437	233	235	154	347	599	5	28
5	1	1	1	1	1	1	2	1	3	453	536	342	235	244	346	599	5	27
6	1	1	2	1	2	2	1	3	4	454	446	343	234	245	446	599	5	31
8*	1	1	4	1	2	2	2	2	3	121	322	231	44–	322	32–	251	4	28
9	1	1	1	1	2	2	1	2	2	446	437	435	245	256	347	599	5	29
11	1	1	1	1	3	2	3	3	3	554	546	453	255	365	347	599	5	36

(Continued on following page)

TABLE 44—*Continued*

Plant no.	Characters (see footnotes and table 12 for explanation of symbols and class values)																	Index values
	PO	PW	PN	PL	PC	Cr	Br	An	FR	Vig SMT	RoW SMT	StN SMT	DFF SMT	LL SMT	StL SMT	Sur SMT	SP	
12	1	1	2	1	3	2	2	3	2	465	447	354	234	367	457	599	5	34
13	1	1	2	1	3	3	3	4	4	551	544	332	234	363	454	593	7	40
14	1	1	2	1	3	2	2	3	2	144	236	233	235	145	146	199	2	28
15	1	1	2	1	3	2	3	2	4	544	436	433	245	475	556	599	5	38
16*	1	2	2	1	3	2	1	4	4	441	434	321	345	354	345	593	7	38
18*	1	1	2	1	3	3	2	3	4	552	444	342	335	255	566	594	7	38
19*	1	1	2	1	3	2	2	5	4	231	434	222	228	244	444	493	3	32
20	1	1	2	1	4	3	3	3	2	566	557	474	334	375	467	599	5	38
22	2	2	2	2	4	2	1	2	5	564	557	332	244	576	466	599	5	42
23	1	1	2	2	4	2	2	3	3	464	457	344	324	364	346	599	5	35
28*	1	1	1	1	1	2	1	3	1	556	446	435	234	356	458	599	5	28
31*	1	1	2	1	1	2	1	3	2	245	337	234	345	247	358	599	5	30
33*	1	1	2	1	1	2	1	2	2	125	226	233	546	133	237	299	2	23
39	1	1	1	1	1	1	1	3	2	146	337	226	444	245	337	199	2	24
52*	2	1	3	2	4	3	3	3	2	163	356	242	343	366	276	199	2	39
65	1	1	2	1	2	3	2	3	1	564	466	572	237	366	576	599	5	34
73*	1	1	1	1	3	3	3	3	2	262	354	252	235	253	374	299	2	32
78*	1	1	2	2	3	2	2	3	2	355	446	343	435	355	347	499	2	30
80*	1	1	2	1	3	3	3	4	4	162	265	121	–45	285	254	194	3	39
84*	1	1	1	1	3	2	3	1	1	454	446	443	444	355	457	599	5	31
89	1	1	2	1	3	2	3	3	1	444	437	442	345	456	446	599	5	33
91	1	2	2	1	3	2	3	3	3	251	343	251	638	454	463	396	3	35
99*	1	1	2	1	3	3	2	3	2	165	357	263	544	375	378	299	2	35
106*	1	1	2	1	3	3	3	2	1	565	557	433	344	465	447	599	5	33
108	1	1	2	1	3	2	1	2	4	452	455	442	234	363	555	496	3	32

109*	1	1	3	1	3	2	3	3	1	266	167	153	–45	285	358	299	2	35
118*	1	1	2	1	3	2	2	3	2	564	565	433	434	575	566	499	2	33
123*	1	1	4	1	3	2	2	3	1	463	544	473	343	454	565	599	5	36
138	1	1	1	1	4	2	2	4	2	553	555	452	246	475	555	599	5	37
143	1	2	2	2	4	1	1	2	2	335	327	223	544	235	338	599	5	31
145*	1	1	3	1	4	3	3	4	3	461	454	332	344	573	555	592	7	43
156*	1	1	1	2	2	..	1	2	1	433	435	322	255	244	335	579	6	29
158*	1	1	2	2	2	..	1	3	1	315	326	224	454	224	337	549	6	29
160*	1	1	1	1	3	2	1	2	2	264	256	242	525	176	356	599	5	31
174	1	1	2	2	4	..	1	3	2	313	215	212	566	124	213	526	8	33
189	1	1	4	2	5	1	1	3	2	453	456	332	344	574	455	599	5	40
197*	1	1	2	4	5	3	3	4	4	441	444	321	385	444	444	491	3	43
198*	2	1	3	3	4	3	3	3	2	564	566	532	335	476	556	595	7	43
206*	1	1	2	5	5	2	2	4	1	555	547	343	346	456	457	599	5	40
209*	1	1	2	1	1	2	2	2	1	445	447	445	334	246	347	499	2	24
216*	1	1	2	1	1	2	1	3	3	454	346	353	345	366	456	599	5	33
225*	1	1	4	1	1	2	1	2	1	224	225	223	656	214	226	569	6	26
226*	1	1	2	1	1	..	1	4	1	125	–27	223	645	135	238	169	1	23
230*	1	1	4	1	2	2	2	3	3	333	325	222	645	164	225	576	8	37
235*	1	1	4	1	2	2	2	1	4	453	445	322	325	354	344	599	5	32
243*	1	1	1	2	4	2	1	2	1	346	437	233	545	144	348	599	5	30
244*	1	1	1	2	3	2	1	2	1	145	237	223	645	146	138	299	2	25
245*	1	1	2	2	4	1	1	2	1	545	437	333	545	334	337	599	5	29
252*	1	1	1	2	2	2	3	4	2	456	347	333	545	355	358	599	5	35
253*	1	1	2	2	3	2	2	3	2	555	447	333	545	267	457	579	6	37
254*	1	1	2	1	3	..	2	2	2	333	225	222	546	224	326	579	6	28
255*	1	1	1	2	3	2	3	3	1	445	337	323	445	245	347	599	5	32
257	1	1	2	1	3	2	1	3	1	354	446	363	335	264	356	599	5	32
262	1	1	2	1	3	2	1	2	2	355	335	254	634	244	347	599	5	29
265*	1	1	2	1	3	2	2	4	1	453	446	332	634	566	567	598	7	37
277*	1	1	2	1	3	2	1	3	1	346	447	334	435	236	348	599	5	28
290*	1	1	4	1	4	3	3	3	4	662	555	342	344	564	777	594	7	45

(*Continued on following page*)

TABLE 44—*Continued*

Plant no.	Characters (see footnotes and table 12 for explanation of symbols and class values)																	Index values
	PO	PW	PN	PL	PC	Cr	Br	An	FR	Vig SMT	RoW SMT	StN SMT	DFF SMT	LL SMT	StL SMT	Sur SMT	SP	
294*	1	1	2	1	3	2	1	2	3	544	436	432	345	356	546	597	7	34
315*	1	1	2	1	4	2	3	3	5	652	545	521	426	556	548	595	7	38
317*	1	1	2	2	2	2	3	4	2	455	447	323	435	385	448	599	5	37
319	1	1	2	1	3	3	2	3	1	255	356	353	535	255	357	399	2	29
351*	2	1	4	4	5	3	3	3	5	662	656	422	215	765	647	593	7	45
357	1	1	4	3	3	..	..	3	5	312	214	211	5–8	215	2–4	546	8	29
365*	2	1	4	2	3	3	3	5	5	662	555	472	243	564	566	593	7	48
367*	2	1	4	2	4	3	1	3	5	351	345	253	545	444	355	592	7	42
374	1	1	2	1	3	..	3	3	5	341	234	232	433	244	246	563	8	38
380*	1	1	2	3	4	2	2	3	2	353	345	232	438	254	233	596	7	36
385*	1	1	4	2	4	3	3	3	2	441	444	321	245	344	444	573	8	40
387*	1	1	4	2	4	3	3	4	1	662	565	531	424	476	654	599	5	39
388*	1	1	3	2	4	2	1	3	1	555	547	333	535	466	447	599	5	34
391*	1	1	2	2	1	1	3	3	5	451	344	234	432	463	568	592	7	40
400*	1	1	2	4	4	1	1	3	1	545	546	323	435	344	437	599	5	32
402*	1	1	3	5	3	2	1	2	2	541	545	322	353	556	434	594	7	38
405*	1	1	1	5	4	2	3	3	2	552	444	343	445	56–	666	592	7	43
406	1	1	2	3	4	2	2	3	1	663	446	552	333	575	555	599	5	37
418*	1	1	2	3	3	2	1	3	2	453	346	231	546	355	356	599	5	35
425	1	2	4	5	4	..	1	1	2	323	426	423	336	337	325	369	1	29
426	1	1	4	5	3	..	..	2	3	312	223	221	628	134	223	539	6	32
432	1	1	2	1	2	1	1	1	3	555	447	343	635	256	457	599	5	30
440	1	1	2	1	4	1	1	2	1	445	436	423	425	544	346	599	5	28
444	1	1	1	1	3	2	1	3	2	544	436	433	244	447	446	596	7	32
446*	1	1	2	1	3	2	2	2	1	565	447	452	544	474	468	596	7	37

453*	1	1	4	1	3	..	1	1	2	222	224	221	534	224	234	557	8	30
454*	1	1	4	1	2	1	2	2	2	333	335	342	535	233	335	599	5	29
457*	1	1	4	1	3	1	2	3	2	455	436	333	535	355	457	599	5	35
465*	1	1	3	1	3	3	2	3	1	566	457	354	434	354	357	599	5	33
468*	1	1	4	1	3	3	3	5	3	531	434	321	332	443	434	591	7	38
473*	1	1	2	1	3	2	1	2	1	333	335	332	537	245	346	599	5	28
484*	1	1	2	2	3	2	1	2	2	245	236	243	645	256	247	499	2	29
491*	1	1	3	4	4	2	2	3	5	141	235	131	745	134	245	273	4	38
497*	1	1	2	2	3	2	1	3	3	332	334	221	448	324	325	573	8	32
506	1	1	2	2	4	3	2	3	5	161	264	271	646	273	264	291	3	40
511*	1	1	2	2	4	2	2	3	1	565	557	453	435	585	457	599	5	37
540*	1	1	2	5	5	2	1	2	2	541	534	321	437	454	333	599	5	35
541*	1	1	4	1	4	3	1	1	2	243	356	232	646	266	356	559	6	36
545*	1	1	3	4	3	2	2	3	2	453	445	232	645	456	547	484	3	35
561*	1	1	2	1	3	..	2	3	5	323	324	322	646	235	436	538	6	34
569	1	1	4	3	4	1	1	2	4	244	247	242	525	367	347	488	2	34

* From reciprocal cross, Oak Grove × Timberline.

PO: orientation of petals
PW: width of petals
PN: notching of petals
PL: length of petals
PC: color of petals
Cr: crown height
Br: mode of branching
An: degree of anthocyanin pigmentation
FR: susceptibility to frost injury
Vig: vigor
(Classes 1 to 6 at the three stations; cf. pp. 138–139)
RoW: width of rosettes at base of plant
(Classes 1 to 6 at Stanford and Mather with class intervals of 15 cm.; classes 1 to 7 at Timberline with class intervals of 5 cm.)
StN: number of flowering stems
(Classes 1 to 7 at the three stations; class intervals 10 cm. at Stanford and Mather, 5 cm. at Timberline)

DFF: date of first flowers
(Classes 1 to 8 at the three stations; class intervals 7 days at all three stations)
LL: leaf length
(Classes 1 to 8 at the three stations; class intervals 4 cm. at Stanford and Mather, 2 cm. at Timberline)
StL: stem length
(Classes 1 to 8 at the three stations; class intervals 10 cm. at Stanford and Mather, 5 cm. at Timberline)
Sur: survival in years
SP: survival pattern at the three stations
(cf. pp. 140–141)
S: at Stanford
M: at Mather
T: at Timberline

and class 8 the longest. The intervals between classes are 4 cm. at Stanford and Mather, and 2 cm. at Timberline, the sizes being smaller at Timberline because the range of variation is smaller there. Class 1 at Stanford and Mather includes leaves 4 to 8 cm. long, and at Timberline leaves 2 to 4 cm. long, whereas class 8 at the lower stations includes leaves 32 to 36 cm. long, and at Timberline, 16 to 18 cm. long.

The plant 160 listed in table 44, for example, had leaves in class 1 at Stanford, class 7 at Mather, and class 6 at Timberline. This plant was, therefore, relatively long-leaved at Timberline and Mather, and very short at Stanford. In contrast, plant 145, which in the table is listed in class 5 at Stanford, 7 at Mather, and 3 at Timberline, was moderately long at Stanford and Mather, and relatively short at Timberline. Such variations in response from plant to plant indicate the extent of the genetic recombinations as expressed on a three-station basis.

The patterns of interstation modification strongly indicate that leaf length is controlled by gene systems operating through physiological processes, and that the speeds of at least some of these processes may vary or become stopped under certain environmental conditions. The marked shifts from plant to plant in the F_2 suggest that the parental races have independently evolved their particular genetic physiological controls. By assuming that the gene systems determining size of leaves are composed of oppositional and complementary factors, either or both of which may be activated or inactivated by factors of the environment, a rational working hypothesis can be reached which, in the present state of our knowledge, accounts reasonably well for the observed resultant effects.

2. Rosette width. The diameter of the basal leafy portion of plants of *Potentilla glandulosa* is a function of the length of the leaves and of the extent of basal branching of the plant. In plants of subspecies *reflexa* the woody caudex determines the basal branching, whereas in *nevadensis* the length of the rhizomes is the determining factor, as is evident from figure 6 on page 17. Most F_2 progeny of the cross Timberline × Oak Grove have a combination of both rhizomes and caudex that varies from individual to individual.

In the transplant gardens the width of the rosettes was determined by measuring the greatest spread in diameter of the basal leafy portion of the plants. Measurements made yearly at each station indicate that for each plant a certain rate of increase in diameter takes place until a maximum size has been attained, after which there is no significant increase, but only minor annual fluctuations.

The figures recorded in table 44 under the notation "RoW" indicating rosette widths are averaged over a period of 5 years at Stanford, and 9 years at Mather and Timberline. The measurements reflect large differences in growth rates of ramets of the same clone at the three transplant stations, and also wide differences among individual plants at any one station. The plants grown at the two lower stations are listed in six size classes with class intervals of 15 cm., and those at Timberline in seven classes with intervals of 5 cm. Class 1 at each station has the smallest rosettes.

Examples of various combinations of widths of rosette found among the F_2 progeny at the three stations can be followed in table 44. Plant 160, for example, is listed in class 2 at Stanford, class 5 at Mather, and class 6 at Timberline, indicating strong growth at the two mountain stations, but relatively slow growth at Stanford. Plant 540 is rated in class 5 at Stanford, class 3 at Mather, and class 4 at Timberline, showing the greatest rosette width at the lowland station.

No attempt has been made to resolve the character rosette width in terms of genic formulas because it obviously is the resultant of the interaction of both genetic and environmental factors, each on a complex level. Width of rosette is a fair indicator of fitness of the individual to the particular environment, so that the figures in column "RoW" of table 44 reflect to a large extent the patterns of success of this sample of F_2 plants in the three climates. The variability in patterns of response among individual F_2 progeny far surpasses the differences between the parents, both of which have the widest rosettes at Mather.

3. Stem length. Stem length is a function of the number of nodes and the length of internodes. These variables are relatively independent of each other, and both are gene-controlled; length of internodes is subject to great modification by the environment. The length of stems largely determines the over-all height of plants of *Potentilla glandulosa.*

At any one station the stem lengths of the Timberline and Oak Grove forms differ from each other strikingly, as shown in figure 25, but both parents are tallest at Mather. At Timberline the Oak Grove parent scarcely ever survives more than a single season, and when it does, it is exceeded in height by the Timberline parent. At the two lower stations Oak Grove is much taller, and the F_2 progeny show strong transgressive segregation, especially at Mather, as is indicated in figure 21. Moreover, individuals that have the same stem lengths in one environment may be modified strongly and in different directions in other environments, as is shown in table 35, page 98.

The recorded stem lengths of the F_2 individuals are based on the means of measurements taken on each cloned plant at each station during each year of the experiment. The plants were then grouped into classes, and the class values for each individual are listed in table 44 in the column under the heading "StL." At Stanford the mean stem lengths of the plants varied between 7 and 61 cm., at Mather between 7 and 70 cm., and at Timberline between 6 and 40 cm. At each station the range of observed variation was divided into classes, the class intervals at Stanford and Mather being 10 cm., and those at Timberline 5 cm. The tallest class represented at Stanford and Mather was class 7, 60 to 70 cm. At Timberline the tallest was class 8, ranging from 35 to 40 cm.

Table 44 shows that many F_2 clones fall into different classes at Stanford, Mather, and Timberline, and that the direction of modification varies from plant to plant. There is a statistically significant correlation between the stem lengths at one station and those at another, however, as will be discussed more

fully later. Like leaf length and rosette width, stem length is obviously the resultant of the interaction of complex genetic and environmental factors.

4. Stem number. The number of flowering stems produced on a given plant is an indication of its vigor and general productivity as well as of its tendency to flower. The number of stems often fluctuates widely from year to year on the same individual at the same station, but the average over a 5- to 9-year period usually reflects its performance with a fair degree of accuracy.

The mean number of flowering stems per individual for a sample of F_2's at each station is listed in terms of classes in table 44 under the column headed "StN." At Stanford the mean number of stems varied between 0 and 40, at Mather between 0 and 60, and at Timberline between 0 and 25. In grouping the plants into classes, class 1 was reserved for essentially nonflowering individuals having a mean number of fewer than 1.5 stems. At Stanford and Mather the remaining class intervals were placed at multiples of 10, with class 2 including plants having a mean number from 1.5 to 10 stems. The highest class represented at Stanford was class 5, ranging between 30 and 40 stems; at Mather the highest class was 7, having 60 to 70 stems. The class interval for the plants at Timberline was set at 5, so that class 2 consisted of plants having an average of 1.5 to 5 stems per plant, and the highest was class 6, having 20 to 25 stems.

Plant 387, for example, is listed in table 44 in class 5 at Stanford, class 3 at Mather, and class 1 at Timberline, indicating relatively heavy flowering at Stanford and poorer flowering with increasing altitude. In contrast, plant 39 is most floriferous at Timberline, where it is in class 6, but flowers poorly at Stanford and Mather (class 2). The patterns of flowering at the transplant stations among the individual F_2 progeny are as complex as those of leaf length, rosette width, or stem length.

5. Vigor. Vigor is a composite expression of the over-all growth, or production of bulk, and is related to such characters as length and number of stems and leaves, width of rosette, mode of branching of the crown, and density of the rosette leaves. Groups of factors are therefore involved in assaying vigor.

Each F_2 individual was rated independently each year at each station on an arbitrary scale, the most vigorous and the weakest plants at a particular station being taken as standards of comparison. Although vigor was necessarily based on subjective judgment, it is perhaps the best general indicator of plant performance at each station. An effort was therefore made to place as accurate and as objective a rating on this character as possible.

At all three stations six classes of vigor were recognized, ranging from class 1 (weak) through class 6 (very vigorous). At Timberline the highest class included plants more vigorous than either parent or the F_1. The averaged ratings for the period of years of the experiment at each station were rounded to the

nearest full number, and are listed in table 44 in the column under the heading "Vig."

Plant 387, for example, is listed in the table with a rating of 6 at Stanford, 6 at Mather, and 2 at Timberline, indicating highly vigorous growth at Stanford and at Mather, and poor vigor at Timberline. Sixteen years after transplanting, this plant had essentially the same relative ratings at Mather and Timberline. Plant 226, on the other hand, has a rating of 1 at Stanford, 2 at Mather, and 5 at Timberline, showing quite the opposite pattern, and these ratings, too, have been confirmed by later observations at Mather and Timberline. Plant 226 is considerably more vigorous at Timberline than the subalpine parent native to that environment.

Later discussion in this chapter will deal with recombinations in patterns of response of vigor as expressed at the transplant stations in terms of machine-selected population fractions, an approach of interest in considering mechanisms of natural selection.

6. Date of first flowers. Among the most characteristic differences between climatic races of widespread species are their seasonal periodicities. The period of flowering is the expression of periodicity that is perhaps easiest to observe. The factors that govern time of flowering are numerous, but genetic factors are clearly of great importance in differentiating this character among the various climatic races.

The parental strains in the cross Timberline × Oak Grove do not differ widely in the timing of their earliest spring flowers when grown at Stanford, the mean difference being only a matter of 7 days, and the F_1 hybrids flower in between. In the F_2 progeny there is a very wide range of segregation in earliness that far exceeds the parental differences, extending approximately 8 weeks, as is shown by figure 22, page 107. The relative order of flowering for any specified F_2 individual is fairly consistent from year to year at a given station, even though variations in weather conditions may shift the flowering period of the population as a whole for as much as 2 or 3 weeks.

The order of flowering of a sample of the F_2 plants at all three stations is listed in terms of classes in table 44 under the column headed DFF. Plant 197, for example, is listed in class 3 at Stanford, class 8 at Mather, and class 5 at Timberline, indicating moderately early flowering at Stanford, very late at Mather, and medium late at Timberline. Plant 426, on the other hand, placed in class 6 at Stanford, class 2 at Mather, and class 8 at Timberline, is relatively late-flowering at Stanford and Timberline, but early at Mather. The random nature of the order of earliness at the three stations for the F_2 plants is evident from the table. Further discussion of the genetic nature of the segregation for earliness will be reserved for later paragraphs.

7. Survival. The length in years of survival at each station is recorded for a sample of F_2 plants in table 44 under the column headed "Sur." Plants that died

within the first or second year after transplanting were replanted, and the average lengths of survival for all the successive replantings are recorded in the table. At Stanford the experiment was terminated at the end of a 5-year period and the plants were removed, but records at Mather and Timberline were continued for 9 years. It is clear from the table that many F_2 plants were incapable of surviving for more than a short period at one or more of the transplant stations, especially at Timberline, whereas other plants were long survivors.

A supplementary experiment designed to test the validity of the above observations with respect to survival and vigor at Timberline was conducted during the years 1950 to 1954. A sample of 91 cloned F_2 individuals that had been growing at the Mather and Timberline stations was divided vegetatively so that three replicated randomized plantings could be made at the Timberline garden. Of the 91 individuals selected, 23 were classified as "weak" at Timberline on the basis of the earlier experiments, 41 as "intermediate," and 27 as "vigorous." The individuals classified as "weak" or "intermediate" were propagated from ramets that had been growing at Mather; those classified as "vigorous" were divided directly from the ramets growing at Timberline. At the end of a 4-year period, all three replicates of 10 of the 23 individuals classed as "weak" at Timberline had died, and only 2 individuals had all replicates living. Among the others, one or more of the replicates had died.

Of the 27 cloned individuals classed as "vigorous" at Timberline, 19 survived in all the replicates over the 4-year period, and all have continued to display good growth. Some losses in the remaining 8 plants were suffered among some of the replicates, but, of the original 81 ramets of this group planted in 1950, 71 survived and were in good growth in 1954. Allowing for accidental deaths, and also for the fact that the propagations within the "vigorous" group were made directly in the Timberline garden without the benefit of prestrengthening by growing them over a winter in pots at Stanford, as were the plants of the "weak" and "intermediate" classes, it is clearly evident that the original evaluation of the various classes of individuals was accurate with few exceptions. The performance of the plants of the "intermediate" class at Timberline likewise paralleled quite closely their original performance.

Very few individuals would have been placed in a different class on the basis of the later experiment. For example, of the 23 cloned individuals grouped as "weak," 2 would have been placed in the "intermediate" class, and 1 individual classed as "intermediate" would have been considered to be "weak." This supplementary experiment, therefore, serves to confirm the validity of the earlier long-term observations that are recorded in table 44.

8. Patterns of survival. In order to visualize more readily the various patterns of survival at the transplant stations, it was found convenient to classify the F_2 progeny according to their recorded performance. For this purpose, two classes were considered at any one station, those having a short survival, and

others surviving the entire experimental period. Plants that survived less than the full experimental period at a given station were classed as "short" survivors, and those with a perfect record as "long."

The F_2 plants were grouped into classes from 1 to 8 on the basis of their survival record at the three altitudinal stations, as indicated at the bottom of table 12, page 51. Class 1 includes plants considered to be the most alpine-like, having "long" survival at Timberline, and "short" at Mather and Stanford. Class 2 consists of plants rated as "long" survivors at both Timberline and Mather, but "short" at Stanford, and includes the subalpine Timberline parent. Class 8, at the other extreme, is composed of individuals having "long" survival at Stanford, and "short" at Mather and Timberline. Class 7, having "long" survival at both Stanford and Mather, but "short" at Timberline, includes the Oak Grove parent.

The intermediate classes represent combinations as follows: class 4, "short" at all three stations; class 5, "long" at all stations, like the F_1; class 6, "long" at Stanford and Timberline, but "short" at Mather; and class 3, "short" at Stanford and Timberline, and "long" at Mather. These classes of survival pattern parallel the classes in the other characters, inasmuch as the Timberline parent belongs to a numerically low class, the foothill parent to a numerically high, the F_1 to an intermediate, and the transgressive variants to the extreme classes 1 and 8.

As is shown at the bottom of table 12, page 51, the highest F_2 frequency falls in class 5, having 148 individuals, all with continuous survival at all three stations. This fact is of interest because neither of the parental races has shown such a high degree of tolerance. It is also noteworthy that the frequencies in the extreme classes are fairly large. Classes 1 and 2, having alpine- and subalpine-like survivals, contain 26 and 56 individuals, whereas those of classes 7 and 8, corresponding in survival to foothill and Coast Range plants, contain 97 and 64 individuals, respectively.

The classes into which individual F_2 plants have been grouped are listed in table 44 in the column under the heading "SP." These ratings enter as one of the 12 numerals used in composing the index value. They indicate the range of tolerance of a given F_2 individual in the three environments, and will be discussed in later paragraphs in connection with characteristics that show correlation.

GENETIC RECOMBINATION AND CORRELATION IN PATTERNS OF RESPONSE

In producing the F_2 population Timberline × Oak Grove, the genes controlling the parental racial characteristics were recombined, and profound changes in genotypic adjustments to environment occurred. The phenotypic expression of each character of each cloned individual in the environments of the three transplant stations provides a measure of this change in genotypic ad-

justment. The responses of a character to these three environments produce a pattern which changes from plant to plant within the F_2.

The study of the interactions of the environment on the genotype of each individual can be facilitated by the use of punched cards in sorting the F_2 plants into classes according to their recombinations in patterns of response at the three altitudes. The following paragraphs will be devoted to such a review regarding three characters—vigor, stem length, and earliness of flowering.

1. Fractions sorted on the basis of vigor in three environments. Vigor is an expression of the bulk of growth; it is the resultant of many integrated processes. For simplicity in sorting, the F_2 progeny were classed in three groups according to their vigor rating at Stanford, namely, weak, intermediate, and vigorous. The "weak" group included classes 1 and 2, as explained on page 138; the "intermediate," classes 3 and 4; and the "vigorous," classes 5 and 6. The same clones were then classified according to their vigor rating at Mather and Timberline determined in a comparable way, and the resulting patterns were tabulated.

If it is assumed that the vigor rating at one station is completely independent of that at the others, and that all possible recombinations exist, the F_2 population would be expected to fall into 27 possible categories. Actually, only 24 of the 27 possible combinations were found, because with regard to vigor there are statistically significant correlations between the performance of a given individual at one station and its performance at another.

The recombinations in patterns of vigor are indicated in figure 31. The graph at the left shows the spread in vigor ratings at Mather and Timberline of the fractions classed as "weak" at Stanford. The numbers intercepting the lines indicate the frequency of individuals having the pattern indicated. The graphs in the center and at the right show a similar breakdown of the groups classed, respectively, as "intermediate" and "vigorous" at Stanford.

Two facts become immediately evident: One is that there is a wide divergence as observed at Stanford. The other is that, despite this divergence, there is a greater tendency for individuals vigorous at Stanford to be also vigorous at Mather and at Timberline than for individuals that are weak at Stanford to be vigorous at Mather and Timberline. There is, therefore, a partial correlation between the degree of vigor of ramets of a group of clones grown at one station and that of ramets of the same clones grown at another. The statistical significance and bearing of these correlations to the genetic structure of climatic races will be discussed a little later.

The chief point of interest in connection with figure 31 is the diversity of patterns shown by the F_2 clones at the three transplant stations. This diversity reflects a wide range of physiological variability, a matter of extreme importance in natural selection. The fact that weakness at one station may be accompanied by either weakness or vigor at either of the other two stations in nearly all the possible combinations indicates that interchanges have taken place between the

parental systems of genes that control the numerous physiological processes basic to growth.

A summary of the combinations in patterns of vigor observed at the three transplant stations is presented in table 45 in the same order as in the graphs, figure 31. The mean rating in vigor at each station of each of the 24 existing groups is listed. For each of the 24 combinations of vigor ratings at Stanford, Mather, and Timberline, the mean length and number of stems, mean survival in years, and mean date of appearance of first flowers at each station are also included. The number of individuals in each vigor combination is listed in column 2 and was used in constructing the graphs in figure 31.

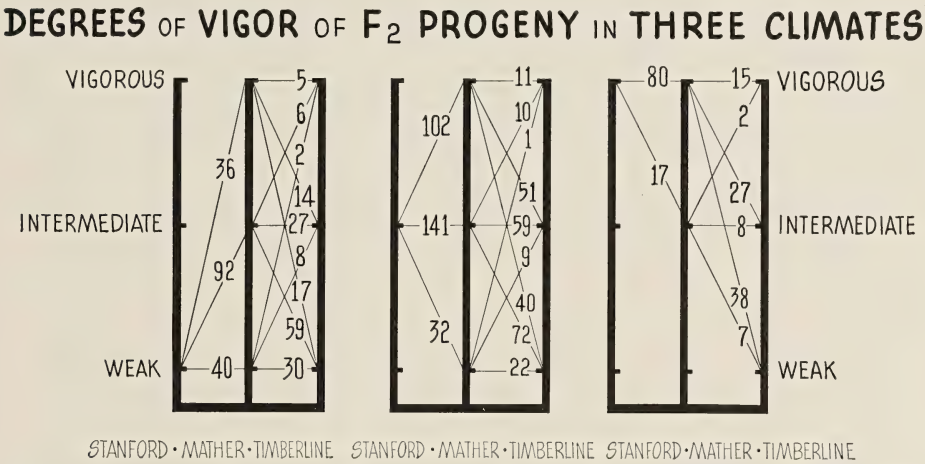

FIG. 31. Graphs showing degrees of vigor of the F_2 clones of Timberline × Oak Grove when grown at Stanford, Mather, and Timberline.

Left, the fraction that is weak at Stanford; *center,* those of intermediate vigor; and *right,* the fraction that is most vigorous at Stanford.

In each graph the scale of vigor at Stanford, Mather, and Timberline is indicated by the three vertical bars; the numbers in the lines show the frequency of F_2 progeny in each category. Note the recombinations in patterns of vigor at the three stations, although statistically there is a partial correlation.

It is evident from table 45 that vigor, length and number of flowering stems, and survival in years are correlated. Such a correlation is to be expected, because length and number of stems, together with the width of the basal rosette, enter into the evaluation of vigor, and vigor is, moreover, an important factor in survival. Earliness of flowering, however, is not correlated with any of these characters, and this fact is reflected in the similarity of mean flowering dates of all the 24 combinations represented. In table 45 there are listed, therefore, examples of characteristics that are partially correlated, and one that is not correlated.

The plants of group 1 of table 45 are weak at all three stations and differ only slightly in stem length from station to station; a clone of this category, number

TABLE 45

PERFORMANCE OF GROUPS OF F_2 PROGENY FROM TIMBERLINE × OAK GROVE SORTED ACCORDING TO VIGOR AT STANFORD, MATHER, AND TIMBERLINE STATIONS

Group no.	No. of plants	Mean vigor rating			Mean length of stems			Mean number of stems			Mean survival, years			Mean date of first flowers		
		S	M	T	S	M	T	S	M	T	S	M	T	S	M	T
1......	31	1.3	1.3	1.2	20.5±2.1	21.1±2.1	18.9±1.7	4.6±1.1	3.1±1.0	1.9±0.4	2.0	2.4	2.8	Apr. 16	May 24	July 29
2......	8	1.9	1.9	3.4	23.1±3.1	23.8±3.3	23.7±1.8	4.2±1.2	3.8±0.9	4.5±1.0	3.9	6.3	7.5	19	26	Aug. 9
3......	2	1.0	2.0	5.0	14.2±3.2	24.8±3.2	36.5±2.0	2.2±0.2	8.9±3.9	9.2±0.9	1.5	7.5	9.0	25	27	5
4......	59	1.6	3.4	1.4	23.6±1.0	31.9±1.0	21.5±0.8	5.0±0.6	10.9±0.7	1.4±0.0	3.2	7.6	4.2	15	24	2
5......	27	1.6	3.6	3.4	21.4±1.8	35.3±1.4	16.0±1.0	5.0±0.8	15.3±1.4	4.7±0.5	2.8	7.5	8.4	16	23	2
6......	6	1.5	4.0	5.2	19.7±2.3	30.2±3.9	33.6±1.7	6.1±1.1	16.2±3.5	13.7±2.3	2.7	8.3	9.0	22	21	July 31
7......	17	1.7	5.4	1.4	25.3±1.4	49.0±2.1	24.5±1.6	6.7±1.1	27.1±3.4	2.8±0.6	2.2	8.8	4.0	16	22	Aug. 2
8......	14	1.4	5.4	3.2	23.3±1.4	46.1±2.3	26.7±1.3	4.4±0.9	25.0±2.6	3.8±0.8	2.7	8.8	8.4	12	20	July 31
9......	5	1.8	5.8	5.2	25.2±2.8	50.7±4.4	34.6±1.9	6.3±2.9	35.3±5.5	6.5±0.8	2.6	9.0	9.0	19	23	29
10......	22	3.2	1.6	1.5	27.6±1.5	21.3±2.6	21.3±1.1	11.0±1.1	3.1±0.6	2.0±0.4	4.5	4.0	3.7	15	26	Aug. 6
11......	9	3.2	1.9	3.1	24.9±2.0	16.3±1.9	23.6±1.4	13.2±2.3	3.3±0.9	4.1±1.1	4.7	6.1	8.2	14	28	4
12......	1	3.0	1.0	5.0	22.8	23.5	31.1	7.8	2.0	14.0	5.0	4.0	9.0			
13......	72	3.3	3.4	1.4	29.5±0.8	32.3±0.9	23.2±0.9	11.0±0.6	10.2±0.7	1.4±0.2	4.7	7.5	4.1	13	25	July 31

14.	59	3.5	3.7	3.3	27.0 ± 0.9	32.2 ± 1.1	25.9 ± 0.5	13.3 ± 0.8	12.2 ± 1.1	4.1 ± 0.3	4.8	8.5	8.2	12	23	Aug. 3
15.	10	3.7	3.9	5.3	25.6 ± 0.6	32.4 ± 1.2	33.9 ± 1.1	18.1 ± 2.8	13.1 ± 1.9	10.5 ± 1.2	4.8	9.0	9.0	14	23	1
16.	40	3.6	5.4	1.4	34.5 ± 1.3	46.6 ± 1.4	24.0 ± 1.0	14.0 ± 1.0	22.8 ± 1.4	2.9 ± 0.5	4.4	8.7	4.1	11	23	1
17.	51	3.7	5.2	3.4	32.2 ± 0.9	44.3 ± 1.3	26.7 ± 0.7	13.8 ± 1.0	23.9 ± 1.6	4.3 ± 0.4	4.7	8.8	8.3	11	23	July 29
18.	11	3.6	5.1	5.1	28.9 ± 1.8	41.6 ± 1.8	33.7 ± 1.0	15.1 ± 1.3	26.7 ± 4.3	9.2 ± 0.9	4.7	8.9	8.6	16	20	Aug. 2
19.	0	5–6	1–2	1–2	No progeny in this group											
20.	0	5–6	1–2	3–4	No progeny in this group											
21.	0	5–6	1–2	5–6	No progeny in this group											
22.	7	5.0	3.6	1.3	37.9 ± 2.8	29.9 ± 3.2	25.9 ± 3.6	17.6 ± 2.6	4.9 ± 0.8	1.7 ± 0.4	5.0	8.6	5.3	11	23	July 28
23.	8	5.0	4.0	3.5	36.0 ± 2.3	35.4 ± 1.5	28.0 ± 1.1	19.8 ± 1.7	13.1 ± 1.4	4.5 ± 0.9	5.0	7.9	7.9	6	22	28
24.	2	5.0	4.0	5.0	31.0 ± 5.0	26.5 ± 1.5	33.1 ± 1.0	17.5 ± 1.5	8.0 ± 3.0	8.5 ± 0.5	5.0	9.0	9.0	15	25	Aug. 2
25.	38	5.2	5.6	1.6	39.5 ± 1.3	48.4 ± 1.2	25.1 ± 1.2	19.8 ± 1.0	23.5 ± 1.9	2.2 ± 0.3	4.9	8.8	4.3	11	19	July 30
26.	27	5.2	5.7	3.4	38.7 ± 1.2	47.8 ± 1.7	27.3 ± 0.6	21.6 ± 1.1	23.9 ± 2.2	3.0 ± 1.1	5.0	9.0	8.2	10	21	Aug. 1
27.	15	5.0	5.3	5.3	33.3 ± 1.2	43.0 ± 2.1	34.1 ± 0.8	18.6 ± 1.5	25.0 ± 2.8	8.1 ± 1.1	5.0	8.9	8.8	18	21	3
Total	505															

453, is illustrated in figure 29. Plants of group 3, which are weak at Stanford and Mather but vigorous at Timberline, are exemplified by clone 226 of figure 27. In contrast to these, plants in group 26 are vigorous at Stanford and Mather and weak at Timberline, as indicated by clone 290 of figure 28. Similarly, each of the 24 groups in table 44 corresponds to a graph line in figure 31.

The three missing classes of the 27 possible combinations are groups 19, 20, and 21. These three categories have the common characteristic of being vigorous at Stanford but weak at Mather. The reciprocal combination, plants that are weak at Stanford but vigorous at Mather, are relatively frequent and are exemplified by groups 7 to 9 in table 45.

The many recombinations furnish convincing evidence that the parental races contain striking evolutionary potentialities that are stored in their germ plasm. Perhaps one of the major evolutionary functions of climatic races is to preserve this variability, which can be automatically released when changed environments threaten the survival of the species.

2. Fractions sorted on the basis of stem length. Among the most conspicuous differences between climatic races are differences in length of stems. In chapter II the complex gene systems that evidently determine this character were reviewed, and the spectacular modifications that may be induced by environment have been discussed in the first pages of the present chapter. The response patterns of the F_2 progeny were grouped into classes according to their stem lengths at Stanford, and the response of each individual in each class was then followed at Mather and at Timberline. The class intervals were 20 cm. at the two lower stations, and 10 cm. at Timberline.

Figure 32 summarizes in graphic form the results of this study. As is shown in the graph at the left, the shortest-stemmed fraction at Stanford contains individuals that are among the tallest fractions at Mather, but the majority of plants in this category were also shorter-stemmed at Mather than the average of the F_2 progeny as a whole. Similarly, the graphs in the center and right of figure 32 indicate the patterns for plants belonging to the taller classes at Stanford. From the recombinations in the station-to-station responses it is obvious that a group of individuals that are similar at one station may possess considerable hidden genetic diversity that appears at other stations. Nevertheless, certain percentages of F_2 individuals belong to the same class of stem length at all three stations, especially in the center classes.

There is a significant correlation between stem lengths at the three stations for the F_2 population as a whole. The correlation coefficient r between stem length at Stanford and that at Mather is 0.476, which statistically is highly significant, although it indicates that approximately 50 per cent of the individuals do not show correlation between stem heights at the two stations. The r value for stem lengths at Stanford as related to Timberline, though only 0.115, is still statistically significant, indicating that about 10 per cent of the individuals show

correlation. Between Mather and Timberline the value of r is higher, 0.212, indicating that approximately 20 per cent of the individuals show correlation.

Stem length is therefore a character in which the expressed heredity at one station has some relation to the heredity expressed by the same individuals at another. At each additional station, however, considerable hidden variability is being revealed. The genetic-physiological systems that regulate stem lengths in *Potentilla* in a series of environments are obviously fairly complex.

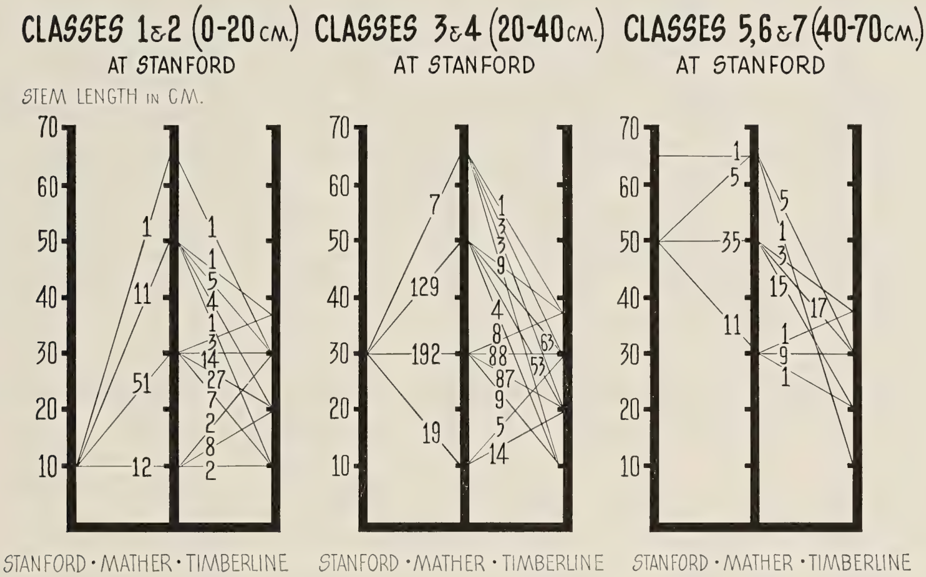

FIG. 32. Graphs showing the recombinations in lengths of stems of F_2 clones of Timberline × Oak Grove at Stanford, Mather, and Timberline.

Left, the fraction that is shortest-stemmed at Stanford; *center,* the intermediate group; and *right,* the fraction that is longest-stemmed at Stanford.

In each graph the scale for stem length at Stanford, Mather, and Timberline is indicated by the three vertical bars; the numbers in the lines show the frequency of F_2 progeny in each category. Note the recombinations in stem lengths at the three stations, although statistically there is partial correlation.

3. FRACTIONS SEPARATED ON THE BASIS OF EARLINESS OF FLOWERING. The order of flowering of the parents, the F_1 hybrids, and the individuals of the divergent F_2 progeny is remarkably consistent at any one station. The spread in flowering time among the F_2 far transcends that of the parents, as was mentioned on pages 107 and 108. However, the relative order of flowering among the F_2 individuals at one station is almost completely independent of that of the same individuals at the other stations.

Four classes of earliness, each having a spread of 14 days, were recognized at each station. These classes were formed by merging by twos the eight classes listed in table 12, page 51. The interstation recombinations as determined by the sorting of punched cards are graphed in figure 33. The numerals inserted

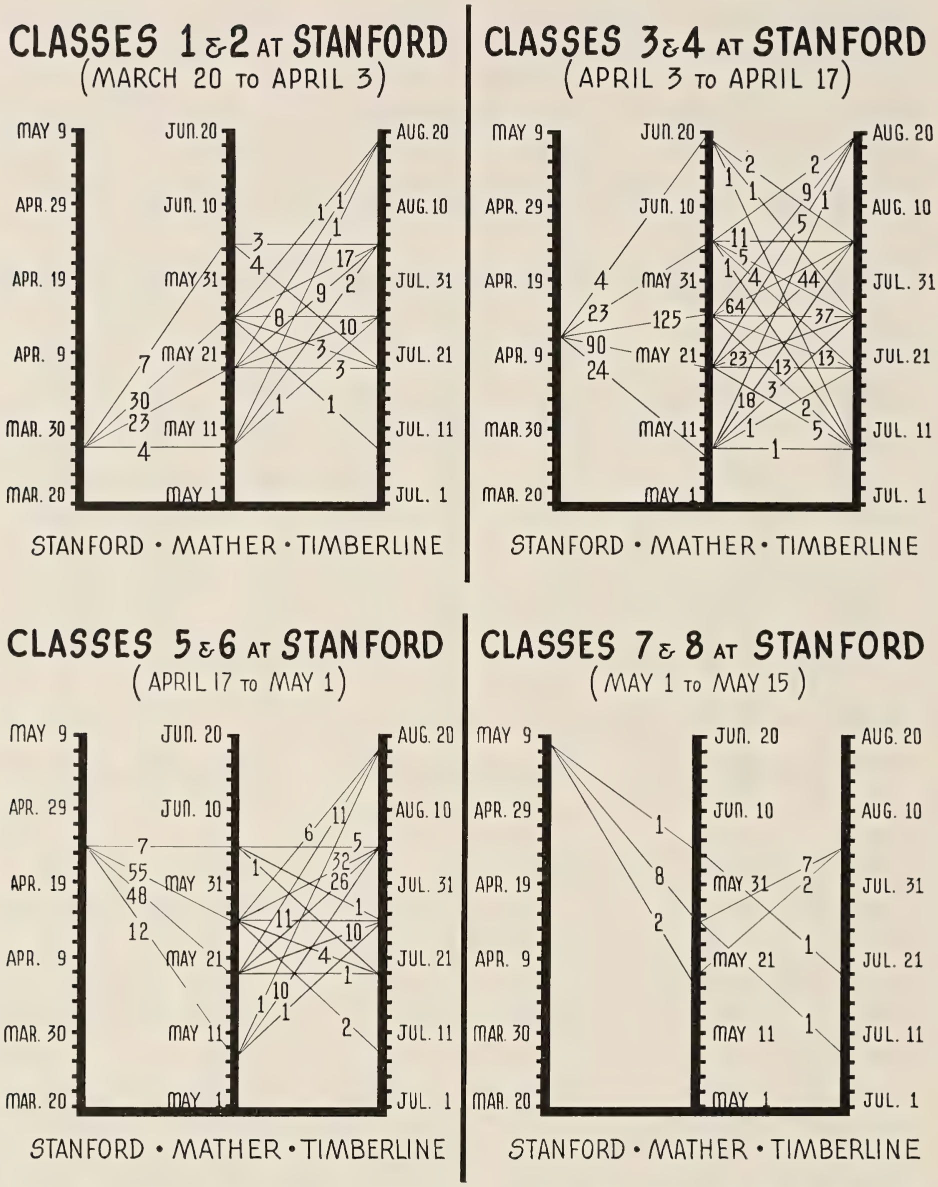

FIG. 33. Graphs showing recombinations in patterns of earliness of the F_2 clones of Timberline × Oak Grove at Stanford, Mather, and Timberline.

Upper left, the fraction of the F_2 progeny that is early-flowering at Stanford; *upper right,* the mid-early fraction; *lower left,* a late-flowering fraction; and *lower right,* the latest-flowering fraction at Stanford.

Numbers in the lines show the frequency of F_2 progeny in each category. There is no statistically significant correlation between earliness at one station and earliness at the other two.

in the lines of the graph indicate the number of F_3 individuals that fall into a particular class.

At Stanford an early fraction, consisting of 64 individuals, started flowering on the average on March 28, as seen in the upper left graph of figure 33. At Mather these 64 individuals separate into four classes, and each Mather class separates again at Timberline, where the spread of the early Stanford fraction ranges between July 7 and August 19. Each of the later fractions at Stanford shows similar recombination at the other two stations, so that some plants that are early at Stanford become late at Timberline, and one plant from the latest class at Stanford ranged among the earliest at Timberline.

Among factors that influence time of flowering at each station are length of winter dormancy, the rapidity with which stored food is transformed into growth during spring, height of stems, and the speed of development from young shoots to flowering stages. Many genetic-physiologic temperature-related processes are involved in this series of developments.

In the snow-free winters at Stanford both of the parental races, the F_1 hybrids, and the F_2 plants undergo a brief period of dormancy beginning approximately the first of January. Spring growth commences between February 15 and March 8, depending upon the race or the particular F_2 plant. The plants of the F_2 vary greatly in their rapidity of growth and in the time at which flowering begins to develop; the average dates of first flowering accordingly range between March 20 and May 15.

At Mather, on the other hand, there are relatively cold winters with minimal temperatures below freezing during 5 months of the year; accordingly, the period of dormancy of *Potentilla* is greater there than at Stanford, and extends from approximately mid-October to mid-April. The spring period is rather brief and the development rapid, the mean dates of first flowering among the F_2 varying between May 1 and June 23.

At Timberline the same cloned F_2 individuals remain dormant from mid-September through mid-June, and flowering of the F_2 plants does not begin until after the first week of July and may range until August 25. In addition to these wide seasonal contrasts between stations, the prevailing temperatures during the growing seasons differ, being in general coolest at Timberline, next coolest at Stanford, and warmest at Mather.

Three facts stand out concerning the variation in time of flowering in the cloned F_2 population of Timberline × Oak Grove: (1) that there is a wide diversity in the patterns of three-station responses; (2) that there is scarcely any significant station-to-station correlation between the F_2 progeny as a whole; and (3) that at any one station there is nevertheless a year-to-year consistency in the order of flowering among distinct F_2 individuals. The last fact indicates that the sequences that lead to the development of flowering are governed by an orderly series of physiological processes. The highly random recombination of flowering patterns of the F_2 population as a whole at the three stations thus

emphasizes the extent of gene recombination governing these physiological processes.

SHIFTS IN CORRELATION FROM STATION TO STATION

Since both highly modifiable and less modifiable characters change their expression from station to station, it might be anticipated that their correlations could also change with the station. To a high degree this is actually the case.

In table 46 are listed 14 characters of the cross Timberline × Oak Grove and their correlations with 2 modifiable characters: vigor and date of first flowers,

TABLE 46

CORRELATION VALUES r BETWEEN FOURTEEN CHARACTERS AND VIGOR AND DATES OF FIRST FLOWERS OF F_2 CLONES IN THREE ENVIRONMENTS

Characters	Vigor: low to high			Date of first flowers: early to late		
	Stanford	Mather	Timber-line	Stanford	Mather	Timber-line
1. Leaf length: short to long	*+0.378*	*+0.804*	*—0.168*	*—0.175*	*—0.223*	*—0.186*
2. Stem length: short to long	*+0.256*	*+0.742*	*—0.237*	*—0.231*	*—0.109*	*—0.203*
3. Stem number: few to many	*+0.240*	*+0.663*	*+0.207*	—0.055	*—0.261*	*—0.143*
4. Survival pattern: alpine to lowland type	*+0.447*	+0.004	*—0.237*	+0.025	*+0.109*	—0.044
5. Vigor at Mather: weak to vigorous	*+0.495*	......	*+0.264*	*—0.130*	*—0.210*	*—0.165*
6. Petal orientation: upcurved to reflexed	*+0.139*	*+0.106*	—0.013	+0.025	—0.017	+0.083
7. Petal notch: notched to entire	+0.018	—0.001	*—0.224*	—0.035	—0.010	—0.020
8. Petal width: wide to narrow	+0.024	—0.044	+0.003	+0.011	*+0.120*	+0.033
9. Petal length: long to short	+0.066	*—0.088*	*—0.190*	*+0.142*	+0.059	+0.078
10. Petal color: white to yellow	*+0.202*	*+0.208*	—0.034	*+0.090*	+0.046	—0.034
11. Crown height at Mather: 0 to 13 cm.	*+0.126*	*+0.341*	*—0.169*	—0.001	+0.024	—0.084
12. Branching at Mather: erect to divaricate	*+0.113*	*+0.344*	*—0.197*	*—0.095*	+0.043	*—0.138*
13. Anthocyanin: green to purple	—0.004	*+0.090*	*—0.238*	*—0.123*	+0.068	*+0.113*
14. Frost susceptibility at Timberline: low to high	+0.033	—0.039	*—0.575*	—0.044	*—0.344*	*—0.187*

Values in italics are statistically significant at the 5 per cent level; others are insignificant.

at the three stations. The statistically significant correlations, which in the table are italicized, vary from station to station.

There is, moreover, a tendency for the correlations at Stanford and Mather to be in the same direction, and at Timberline in the opposite direction. Commonly, the correlations are positive at Stanford and Mather, and negative at Timberline. An exception is the correlation between degree of anthocyanin and date of first flowers, in which the Stanford data show negative, and the Timberline data positive, correlation.

The correlations may also be in the same direction at both the low- and the high-altitude stations. Leaf length, stem length, stem number, type of branching, and frost susceptibility all show negative correlations with respect to date of first flowers at low and high altitudes, but the strengths of the correlations vary from station to station.

A special case is the strong negative correlation between frost susceptibility at Timberline and high vigor. It is evident that the highly susceptible plants would lose vigor at Timberline by direct effect rather than by genetic linkage. These two characters are not correlated at the other two stations.

Another special case concerns the high correlations between vigor and leaf length, stem length, and stem number. Plants having long leaves and many and long stems tend to be classified as vigorous. At Timberline, nevertheless, the correlations are negative, high vigor being correlated both with small leaves and with short stems. In this example the reduction in vigor caused by small leaves and short stems is compensated by the width of the basal rosettes and by the number of leaves and stems. A high number of stems is one of the few characters that show positive correlation with high vigor at Timberline.

It is evident that there is no general rule governing interstation shifts in correlation. The reason for the interstation shifts apparently lies in the complex gene systems that regulate the characters of ecological races, as was discussed in chapter II, pages 117 to 122. The rather frequent cases in which the correlation at Timberline is in a direction opposite to the correlations at the two other stations strongly suggest that genes other than those expressed at Stanford and Mather become activated in the Timberline environment.

It does not follow that shifts in correlation in contrasting environments are caused by a variation in degree of linkage under these conditions. The correlations result from ratios in phenotypic expression of the genotypes, and not from a difference in proportion of segregated genotypes.

CORRELATION BETWEEN SURVIVAL CAPACITY AND PARENTAL CHARACTERISTICS

Plants that survive in a given environment are able to maintain a long-range positive balance of growth. The annual increment may be low, as, for example, in F_2 progeny that are not able to attain maximum size at Timberline until after 12 years, whereas faster-growing individuals at this same station may attain

maximum equilibrium size within 6 or 7 years. At Mather and Stanford, the rate of increase in the same clones is usually considerably greater than at Timberline, full size being attained 2 to 4 years after transplanting. Since the capacity of distinct F_2 individuals to grow successfully at the three stations varies widely among the recombinations, it is of interest to determine whether there is a tendency for progeny most resembling the Timberline parent to be successful at the alpine station, and for progeny most resembling the Oak Grove parent to survive best at the two lower stations.

The degree of resemblance of an F_2 individual to either parent can be determined approximately and rated on an arbitrary scale. The rating according to index value, as explained on pages 49 and 52, is reasonably objective and can be used as an approximate measure of degree of relationship. Obviously it is

TABLE 47

PERCENTAGES OF LONG-PERIOD SURVIVORS AT THREE TRANSPLANT STATIONS AMONG THREE CLASSES OF F_2 PROGENY HAVING DIFFERENT INDEX VALUES

Classes of index values	Characterization of index classes	Percentages of long-period survivors			No. of clones
		Stanford	Mather	Timberline	
20 to 29	Most subalpine-like	17.8	49.5	75.6	90
30 to 39	Intermediate	77.0	71.5	34.3	330
40 to 50	Most foothill-like	70.8	76.5	13.5	89
All index classes combined		65.5	70.5	37.9	509

Long-period survivors are ramets of clones that survived at a station over the entire experimental period (5 years at Stanford, 9 years at Mather and Timberline) without replacement.

only a rather rough approximation of the infiltration of genes by one parent as compared with the other, because the index does not specify parental proportions.

In table 47 the percentages of F_2 individuals surviving for long periods are listed for each station and for each of three ranges of index values, namely, 20 to 29 (the most subalpine-like in index value); 30 to 39 (intermediate); and 40 to 50 (most foothill-like). Ramets of clones that survived through the experimental period at any one station were classed as long-period survivors; those requiring one or more replantings, as short-period survivors (essentially nonsurvivors).

It is evident from table 47 that plants belonging to the class having low index values (20 to 29) have the highest percentage (75.6) of survival at Timberline, and the lowest (17.8) at Stanford, whereas plants most resembling the foothill parent in index value have the highest survival percentages at Stanford and Mather (70.8 and 76.5, respectively), and low (13.5 per cent) at Timberline. The large intermediate class, which includes individuals bounding both the

extremes, survives best at the lower altitudes, but also is moderately successful (34.3 per cent survival) at Timberline.

A distinct genetic coherence therefore exists between the 12 indexed characteristics of the natural parental races and the capacity of their progeny to succeed either in specialized environments or over a wide range. Although none of the parental morphological types were segregated, there is clearly a tendency for the types most resembling the parental races to be most successful in the kinds of environment occupied by the particular race.

SELECTION OF SPECIFIED FRACTIONS OF F_2 PROGENY

In a segregating F_2 population having the complex recombination patterns observed in Timberline × Oak Grove, it should be possible, on the basis of the available data, to screen those individuals that are adjusted to succeed in a specified climatic zone. For the purpose of illustrating the possibilities for diversified selection in this F_2, selection may be performed by means of punched cards after the specifications have been drawn.

Three groups were thus selected among the F_2 progeny of Timberline × Oak Grove. One of these was intended to include individuals best suited for long-range survival in the high altitudes of the Sierra Nevada; another group, those best suited to the low California Coast Ranges; and a third group, plants having exceptional capacity to survive over a wide range from low to high altitudes. The last two groups fall outside the range of the parental races.

The specifications for the selections are listed in table 48. The plants of each group thus selected are listed by number in table 49, and the characteristics of the selected individual plants can be followed in detail in table 44. In table 49 the selected plants are grouped according to their index value, which gives some measure of the degree of relationship of the selected plants to the parental races.

The group selected as adjusted to an alpine environment consists of 30 individuals. All of them have index values higher than 19, the value of the Timberline parent, and all these synthetic "alpines" are taller and have longer leaves than the natives at Timberline. Many also flower earlier and are less subject to frost injury than the Timberline parent, which itself is among the earliest and most frost-hardy of the native population.

Only 12 of the 30 plants selected as being highly successful at Timberline have an index value below 30, and the values of the remaining 18 plants range between 30 and 39. The latter group represents a blend of subalpine and foothill characteristics. It is noteworthy that not a single individual of this fairly large sample successful at Timberline had an index value of 40 or above. Each one of the "synthetic" alpines," however, contains a number of characteristics inherited from the foothill parent, and these seem to have contributed something to the success at the high altitude of this group of reconstituted "alpines." All except one of the machine-selected individuals of this alpine group still survive

TABLE 48

Basis of selection by sorting machine of three groups of F_2 progeny capable of survival in specified environmental zones

Character	Classes* specified				
	For Coast Range climate: Stanford only	For highly diverse climates:			For alpine climate: Timberline only
		Stanford	Mather	Timberline	
Vigor	5 to 6	4 to 6	5 to 6	4 to 6	5 to 6
Stem length	5 to 8	4 to 8	5 to 8	6 to 8	7 to 8
Date of first flowers.....	1 to 3	.....	.....	1 to 5	1 to 5
Survival in years........	5	5	9	9	9
Frost susceptibility	.....	.....	.....	1 to 3	1 to 2

* Classes refer to categories of each character as shown in table 12, page 50; where no classes are indicated, none were specified.

TABLE 49

F_2 individuals, listed by number, selected by sorting machine on the basis of their performance at three transplant stations. The selected individuals are classified according to their index values.

Machine-selected groups; cf. table 48	Groups of index values			Total individuals selected
	23 to 29, alpine-like	30 to 39, intermediate	40 to 50, foothill-like	
For Coast Range climate.......	....	15, 65, 138, 294, 406	198, 351, 365	8
For highly diverse climates.....	....	12, 20, 84, 216, 511	206	6
For alpine climate.............	9, 28, 39, 158, 209, 226, 244, 245, 262, 277, 319, 484	12, 20, 31, 78, 99, 106, 109, 143, 243, 252, 253, 255, 317, 388, 400, 457, 465, 511	....	30

with continuing vigor at Timberline at the present writing, 18 years after transplanting. The exception, plant 400, died after having been moved to a new location in the garden in 1950.

Among the group selected as being most highly tolerant to conditions in the Coast Ranges are 8 individuals which, in many respects, respond like forms of subspecies *typica* native there. None of these plants has an index value below 30, and 3 of the 8 selected have values between 40 and 50, which approach the value 54 of the Oak Grove parent. Of interest is the fact that none of these 3 is a survivor at Timberline, whereas 4 of the 5 having index values 30 to 39 survive indefinitely there.

The group selected as highly tolerant—successful at low, intermediate, and high altitudes—consisted of 6 individuals. None of these had an index value below 30, and only 1 had a value of 40. Morphologically there was a trend in this group toward the foothill parent, although the success of these plants at Timberline was considerable. Three plants belonging to this group of high tolerance were also included in the alpine group.

In setting up the specifications for these three selected groups of plants, the requirements were purposely drawn at a highly restrictive level, and tended to include only individuals outperforming the parental types. Many recombination types of unusual performance doubtless have been excluded.

In the groups selected for alpine and for Coast Range conditions, 20 among 30 of the former and 4 among 8 of the latter survived indefinitely at all three stations, although in making the selections no attention was paid to their performance at stations other than either Timberline or Stanford. This is a somewhat higher percentage than for the F_2 population as a whole; among 484 individuals that have a record of long survival at least at one station, there are only 148 that survived indefinitely at all three stations. The occurrence of broadly tolerant forms in the strictly specified selections is a consequence of the general genetic coherence among characters differentiating the races.

CONCLUSIONS

Two principles appear to have operated in the evolution of natural races for contrasting environments. One is that such races have a mechanism enabling them to attain a certain degree of genetic coherence in racial characteristics. The coherence tends to preserve the germ plasm in fairly well defined biological entities that are capable of surviving in their respective environmental zones. The other principle is that the genetic coherence is flexible, because the characters are not so tightly bound as to impede extensive recombination of the germ plasm. If major changes in the environment occur causing changes in selective pressures, opportunities for intercrossing between distinct ecological races are likely to increase, leading to greatly enhanced genetic diversity.

Such a genetic structure makes it possible for plants of neighboring races to occur in adjacent but ecologically distinct habitats and yet remain recognizable

entities, as described in chapter I. Crossing may be fairly infrequent between distinct races in adjacent habitats because they may differ in their time of flowering as well as in their ecology.

The present races are the products of long-time selection, and have attained an equilibrium with their environments. Natural selection will therefore tend to favor the original racial combination as long as the over-all genetic structure and the habitats remain the same, although a certain amount of introgression may take place. Over long periods genes may gradually migrate across long distances from the original point of contact and may finally appear in combinations where they have selective value.

IV

SYSTEMS OF GENES CONTROLLING CHARACTERS AND THEIR SIGNIFICANCE IN ENVIRONMENTAL ADAPTATION AND EVOLUTION

At the dawn of experimental genetic investigations, beginning with Gregor Mendel and with the rediscovery of two of the basic principles of heredity at the beginning of our century, the relation of the gene to the individual character was thought to be a simple one. In the early years of the century many biologists even believed that the inherited units regulated only peripheral characters of the organism. Genetic information accumulated at such a remarkable pace during the first decade of the century, however, that by 1910 one could begin to sense that genes controlled the development of many characters of the organism. Also, evidence had been discovered that an individual gene could influence several related characters, and that the development of each character could be controlled by several distinct genes.

Before the first decade had passed, not only the principles of dominance and of intermediate inheritance were known, but also the effects of genes having complementary, suppressive, or inhibiting effects, and the action of polymeric or multiple genes having either additive or subtractive effects on a character.

Moreover, the action of genes having epistatic or covering effects on other genes in the series, and the genetic basis of transgressive segregation, were beginning to be understood. The phenomenon of genetic linkage first known under the term "reduplication" had been discovered. The concept of blending inheritance, which was discussed by the early hybridizers on the basis of their observations on hybrids between wild species, had received a new interpretation in Mendelian terms.

Many of the early geneticists had a background in physiology and therefore conceived of the genes in terms of functions, processes, and development. The relation of genes to physiological processes had been suggested as early as 1905 by Bateson, Saunders, Punnett, and Hurst. Some of the early geneticists therefore had serious misgivings when, through the enlightening investigations of Morgan and his associates during the next decade, genes were associated with the chromosomes, especially with definite loci. At that time the chromosome was thought of as a purely morphological structure, not as a bundle of biochemistry. The pioneers in genetics feared that a misconception of genes as having specific morphology might develop rather than the concept that genes are associated with processes or specific chemical functions. In retrospect, it is now evident that the concepts of the two schools were not antagonistic, but complementary.

Throughout the first quarter of the century some influential geneticists still thought of genes as providing kinds of embellishment or of extra ornament for the organism, but were unwilling to admit that they controlled the most

vital processes. The physiological group among the geneticists still maintained that genes might control varietal and subspecific characters, but they felt convinced that species differences were cytoplasmic and not chromosomal. It was not until Heribert-Nilsson's classic genetic analysis of interspecific hybrids within the genus *Salix* (1918) and the genetic analysis of species differences in *Melanium* violets (Clausen, 1922, 1926) that it became evident that even those characters that distinguish species are of the same nature as those that distinguish entities below the species level. The extreme defenders of cytoplasmic control of species differences then retreated to the genus level for the application of their theory.

The idea became prevalent around 1930 that most of the problems concerning the genic control of characters had been solved; the genes also appeared to be solidly embedded within the chromosomes, so that this field could be left alone. Attention was therefore turned more toward the nature of the gene and its mutability. This change in emphasis was both timely and natural. The strong emphasis upon the individual gene, however, almost completely obliterated the memory of the extremely fruitful approach through the analysis of the genic control of specific characters, and of the genetic structure of distinct organisms. In studies on evolution and the processes leading to the differentiation of distinct races and species, it is obvious that the genetic mechanisms that control the expression of characters in distinct environments must be examined.

Because geneticists have generally accepted the premise that environment influences the expression of genes, investigations on the influence of distinct environments have been almost entirely omitted from systematic genetic studies. Environment usually is kept as uniform as possible so that variations caused by gene differences can be studied. This limitation in the usual experimental approach has resulted in a gap in our basic genetic knowledge. The responses of cloned F_2 individuals of the interracial hybrid of *Potentilla glandulosa* in three contrasting environments discussed in chapters II and III emphasize this gap in our knowledge.

A new field of study utilizing controlled heredity in controlled sets of environments would doubtless lead to a much more precise understanding of gene action than has yet been attained. The subject of environmental modifications in plants was discussed during the development of the early concepts of the phenotype (Johannsen, 1903, 1909, 1911), and it has been clearly elucidated again from the zoological viewpoint in Goldschmidt's discussions on phenocopies (Goldschmidt, 1935*a,* 1935*b,* 1938), although the concepts of phenocopy and phenotype are not interchangeable. It is now clear that a much enriched conception of the genetic control of characters can be obtained through the responses of cloned individuals of segregating populations of plants grown in contrasting environments.

Many geneticists have sensed the limitations in the study of the expression of individual genes in a standard laboratory and garden environment. They have realized that our concept of evolution will be biased if it is based solely upon

observations under laboratory and garden conditions. The feeling of this limitation has led to a new approach by a branch of population genetics. The mathematical theories for this approach were developed by Fisher (1930) and by Wright (1931). This approach has been useful in that it has served to bring geneticists out of the laboratory into the field. An outstanding population analysis has been that of the frequencies of chromosomal strains of the two species *Drosophila pseudoobscura* and *D. persimilis* along the central California transect of the Sierra Nevada (Dobzhansky, 1948).

Considerable controversy has arisen between the advocates of mathematical theories of evolution advanced by Fisher and by Wright. The major difficulty in applying such theories in field tests on natural populations lies in the fact that very little is known about the basic genetic structure underlying ecologic races. It therefore seems premature to discuss the relative merits of formulas that are designed to by-pass a detailed genetic analysis, particularly since from available evidence the genetic systems these formulas assume are far too simple to represent correctly the operation of actually existing systems. Nevertheless, both mathematical theories have made a valuable contribution in providing working models of what could happen in a population under certain simplified circumstances.

A very active and highly promising phase in contemporary genetics has been the biochemical approach, which visualizes genes as enzyme producers. This development was foreshadowed during the first decade of the century, but has come to fruition mainly during the past two decades. The simplest form of this approach is the study of heritable deficiencies in metabolism requiring the addition of certain biochemical constituents to the nutrition; it is beautifully exemplified in Beadle's *Neurospora* work (1949), and in Lindegren's experiments with yeast (1949). Another approach to the biochemical concept of gene action is exemplified in Winge's analysis (1949) of the systems of genes that in certain species of yeast synthesize specific enzymes which, in turn, effect the fermentation of specific sugars. The object in Winge's study was to analyze the genetic basis of certain physiological characters of an organism rather than to study the mode of action of individual genes.

Relatively little is known about genes that govern physiological processes and the manner in which such processes are influenced. The connection between genes and processes presumably is through biochemical substances such as enzymes, hormones, and other organic compounds. The physiological processes, in turn, are greatly influenced by environmental factors such as temperature. The key to a fuller understanding of the mechanisms of evolution and adaptation will probably be found through detailed studies on the interaction of the genetic, physiologic, and environmental systems. Thus far only scattered attempts in this direction have been made toward an understanding of the relations between genes and physiological processes on the one hand, and on the other between specific processes and the performance of the plant under various environments. Until adequate basic information along these lines on

the genetic systems of wild plants has been gathered, our understanding of the mechanisms of evolution will remain incomplete at vital points.

GENETIC SYSTEMS REGULATING INDIVIDUAL CHARACTERS

Because of the relative scarcity of information on gene systems regulating individual characters, it is timely to re-examine the evidence from some of the outstanding genetic investigations during the first ten years of the present century, and to re-evaluate the conclusions in the light of data of later origin. In so doing we shall follow a historic development of genetic concepts.

COMPLEMENTARY GENES IN LATHYRUS ODORATUS L. It was soon after the rediscovery of the Mendelian laws that Bateson, Saunders, and Punnett (1906) in one of their classic *Reports to the Evolution Committee* proposed an acceptable Mendelian explanation for a puzzling observation that a hybrid between two white-blossomed forms of the Emily Henderson sweet pea of the Leguminosae produced bluish flowers. Although the parental white forms were phenotypically alike, and separately produced only white progeny, each possessed something different that could supplement the other so that color could develop when the heredities of the two were brought together in a hybrid. The authors suggested that the genetic differences between the parental forms, the F_1, and and F_2 were as shown in table 50.

In the formulas of the table the letter C denotes one basic gene necessary for the production of colored flowers, and R another gene necessary for color and complementary to C. Color is not produced unless both these dominant genes are present. Only 9 out of 16 F_2's possess both the C and the R gene and become colored, so that there will be 9 colored to 7 white. If, in addition to C and R, the dominant B gene is also present, the color becomes blue; plants without B (bb) are red.

In this simple system the genes are interdependent: C and R cannot come to expression unless both are present, and the gene for bluishness, B, cannot express itelf unless both C and R are present.

Bateson, Saunders, and Punnett sensed the biochemical significance of such complementary types of hereditary mechanisms, for they stated in a footnote (1906, p. 31):

> The behavior of these two factors strongly suggests that one of them (C) may be the colour-forming stuff which gives rise to colour when acted upon by the other factor (R). We should then have to regard this latter as of the nature of an enzyme, but, in the absence of direct chemical evidence, we consider it advisable to use noncommittal terms for the present.

It is of interest to note that in their 1906 report (p. 4) the authors also called attention to the presence of dominant bleaching genes in both *Matthiola* and *Lathyrus,* so that even at this time keen observers were aware that light colors could be either recessive or dominant.

COMPLEMENTARY AND INHIBITORY GENES GOVERNING COLOR OF PLUMAGE IN POULTRY. The principle of complementary genes was soon extended to the animal kingdom, for Bateson in co-operation with Punnett (Bateson, 1909) showed that poultry have two kinds of white, both recessive. The two are exemplified by White Rosecomb Bantam and White Silky fowl. When these whites were crossed, they produced a colored F_1, and the F_2 progeny segregated in the ratio of 9 colored to 7 white, as in the two kinds of sweet peas. Bateson designated the two complementary genes for color in fowl as X and Y.

Poultry were found also to possess a third kind of white that is dominant. When White Leghorn was crossed with White Silky, the F_1 was white, but in the F_2 both colored and white progeny were obtained. The genic analysis of the F_2 had not been completed by 1909, the date of publication of *Mendel's*

TABLE 50

INHERITANCE OF FLOWER COLOR IN SWEET PEAS (DATA FROM BATESON, SAUNDERS, AND PUNNETT, 1906)

White, CCrrBB——×——White, ccRRbb
F_1: bluish, CcRrBb

FREQUENCIES IN F_2

Phenotypes and genotypes	Observed	Calculated	Ratio
Blue, CRB	1634	1571.5	27
Red, CRbb	498	523.8	9
White, Crr··, ccR··, ccrr··	1593	1629.7	28
	——	——	—
Totals	3725	3725.0	64

Principles of Heredity, but Bateson indicated that White Leghorn possesses both the X and Y genes that are necessary for the production of colored plumage, and that, in addition, this breed contains also a dominant suppressor for color, namely S, so that the Leghorn formula would be SSXXYY, and that of White Silky fowl ssxxYY. Accordingly, both parents are homozygous for Y, so that the cross White Leghorn × White Silky is the prototype for the ratio of 13 white to 3 colored, and for a simple gene system composed of genes with opposite effect.

POLYMERIC GENES IN WHEATS AND OATS AND TRANGRESSIVE SEGREGATION. One of the major objections to the acceptance of Mendelian principles in explaining natural variation and evolution was the fact that early investigations in genetics were concerned with variation in discernible and classifiable steps, whereas it was general knowledge that within the species most characters show continuous variation.

This gap in Mendelian theory was bridged by Nilsson-Ehle's two papers on hybridization of oats and wheats (1909, 1911). The extensive hybridizations that led to the discovery of these new principles were started at the Swedish plant-breeding station of Svalöf in 1900, the year of the rediscovery of Mendel's papers. Nilsson-Ehle crossed strains having contrasting grain colors, namely, black and white in oats, *Avena sativa* L., and red and white in wheat, *Triticum vulgare* L.

The inheritance of color in grain proved unlike color inheritance in sweet peas and in fowl: the F_1 progeny from four separate crosses between white and red were somewhat intermediate, being less red than the paternal parent. Three of the crosses in the F_2 segregated 3 red to 1 white. The fourth hybrid, white crossed with the red Swedish Velvet wheat, yielded only 6 F_1 plants, all red. The 6 selfed F_2 progenies produced a total of 384 plants having various shades of red, but no whites.

For testing the third generation, Nilsson-Ehle selected one of the 6 F_2 progenies, which consisted of 78 plants, all red, and produced 78 F_3 progenies from it. Most of the F_3's remained red, but some segregated into various shades of red and white. Each wheat plant produced only small progenies; the size of the F_3 progenies ranged between 4 and 167 plants per F_2 parent. Some F_2 plants segregated in a ratio of 3:1, as, for example, one having a progeny of 38 red and 12 white plants. But frequencies like 52:4, 37:2, 25:2, and 15:1 were found, in addition to others having even smaller proportions of white, such as 61:1, 51:1, 52:2, and 125:2. Such frequencies could not be explained on the basis of the then current theories.

Nilsson-Ehle concluded that the Swedish Velvet wheat possessed at least three pairs of genes for the production of red color, R_1 to R_3, and that any one of these R genes could independently produce red grain color, so that only the triple recessive, $r_1r_1r_2r_2r_3r_3$, would be white. The F_2 should therefore segregate in the proportion of 63 red to 1 white, the 63 consisting of various shades of red, depending upon the number of R genes present in the F_2 plant. Among 78 F_2 plants there was a reasonable expectation that the triple recessive might not occur. Looking backward from the vantage point of the year 1956, it seems more likely that at least four pairs of dominant R genes operated in some of the other 5 F_2 families of this combination, or even in the family from which the F_3's originated. Assuming that only three multiple pairs of genes segregated, the statistical probability is fairly remote of not finding a single white plant among 384 F_2 plants of 6 families.

The 78 F_3 progenies stemming from the 1 F_2 family were classified according to their apparent ratios of segregation as shown in table 51, except that in Nilsson-Ehle's original paper the calculated ratio for 78 F_2 families was not given, nor were the totals listed. The ratios were calculated on the basis of 64, not of 63, as they should have been, because all the F_2 parental plants belonged to the red class. These data have repeatedly been copied without the error's being noted. The agreement between the observed and calculated ratios is therefore

actually considerably better than Nilsson-Ehle assumed, although the table shows that there are too many constant red progenies, and too few segregated in the ratio 63:1. This discrepancy is to be expected because several of the non-segregating F_3 progenies were not large enough to register a segregation of 63:1.

Nilsson-Ehle investigated also the inheritance of color in the spikelets of oats; he found that there were four major steps in color, namely, black, gray, white, and yellow. Each color covered the next in the order listed. In one of the crossings, black was found to be controlled by two multiple genes.

If Nilsson-Ehle's data are reinterpreted on the basis of current concepts, it seems apparent that oats possess an epistatic series of at least four or five pairs of genes determining spikelet color. Evidence supporting this hypothesis is furnished by four crossings which supplement one another, data from which are

TABLE 51

SEGREGATION OF GRAIN COLOR, RED TO WHITE, AMONG F_3 PROGENIES OF WHEAT FROM RED F_2 PLANTS (DATA FROM NILSSON-EHLE, 1909)

Kinds of F_3 ratios	No. of F_3 progenies		
	Observed	Calculated	Ratio
All red	50	45.9	37
63 : 1	5	9.9	8
15 : 1	15	14.9	12
3 : 1	8	7.3	6
Total	78	78.0	63

Calculation of frequencies is based on the assumption of three pairs of multiple genes segregating in the F_2.

listed in table 52 with accompanying genetic formulas assigned by the present authors.

The most basic (i.e., hypostatic) recessive color for the *Avena* spikelets is yellow, which is covered by any one of the other colors, even white. We may designate this homozygous yellow background color as YY. The yellow can be bleached by a partially dominant but epistatic whitening gene, W, which changes yellow into white. In turn, both yellow and white are covered by an epistatic gene for gray color, Gr, which is not completely dominant, so that two Gr genes are needed to cover completely the yellow or white. Finally, either one or all of the colors already mentioned can be covered by two polymeric and epistatic genes for black or brown, S_1 and S_2. The effects of these last are cumulative, so that only $S_1S_1S_2S_2$ is fully brownish black, and plants that are recessive for one to three of these genes have spikelets of various shades of brown.

Nilsson-Ehle (1909) further found in *Avena* that the presence or absence of a membranous ligule at the junction of the leaf blade and its sheath is also governed by a series of multiple genes. The shape of the ligule in many grasses

is a character used to indicate species differences. A strain of oats without a ligule, "Jaune géant à grappes," was crossed with five other strains having ligules. The F_2 and F_3 segregations indicated that one of the ligulate strains had only one dominant gene governing the presence of ligule, another strain had two multiples, two strains had three, and one probably four pairs.

TABLE 52

SEGREGATION FOR COLOR OF SPIKELETS IN OATS (AFTER NILSSON-EHLE, 1909)

F_2 FREQUENCIES AND RATIOS OF COLOR CLASSES

F_1 combination	Black $S\cdots Y$	Gray $s_1s_2Gr\cdot Y$	White s_1s_2grWY	Yellow s_1s_2grwY	Totals
Black × *white* (9 crosses)					
$S_1s_2grWY \times s_1s_2grWY$					
Observed	2468	...	795	..	3263
Calculated	2459.3	...	813.7	..	3263.0
Ratio	3	...	1	..	4
White, 0315 × *black, 0670*					
$s_1s_2grWY \times S_1s_2GrWY$					
Observed	418	106	36	..	560
Calculated	420.0	105.0	35.0	..	560.0
Ratio	12	3	1	..	16
White, 0353 × *black, 0668*					
$s_1s_2grWY \times S_1S_2GrWY$					
Observed	630	40 (gray to white)		..	670
Calculated	628.2	41.8		..	670.0
Ratio	60	3	1	..	64
Black, 0401 × *yellow, 0101*					
$S_1s_2grWY \times s_1s_2grwY$					
Observed	172	...	34	19	225
Calculated	168.7	...	42.2	14.1	225.0
Ratio	12	...	3	1	16

Y: gene for yellow; hypothetical basic gene for color; all plants are YY.
W: whitening gene for Y, semiepistatic over Y.
Gr: gene for gray color, epistatic over W and Y, but hypostatic under S.
S_1 and S_2: dominant, cumulative, epistatic genes for black; intermediate types are brown.

The normal pyramidal panicle type of inflorescence of oats, having branches in all directions, was found to be regulated by at least three multiple pairs of dominant genes, A_1 to A_3. The fewer A genes the plant possesses, the stiffer and more erect the branches of its inflorescences are. Plants that are purely recessive, $a_1a_1a_2a_2a_3a_3$, have a unilateral, stiffly erect so-called "banner" type of inflorescence. When two strains were crossed that had fairly stiffly erect but pyramidal panicles controlled by different A genes, as, for example, the combination $A_1A_1a_2a_2a_3a_3 \times a_1a_1A_2A_2a_3a_3$, the variation in F_2 extended beyond that represented by both parents. Plants having one-sided banner inflorescences, $a_1a_1a_2a_2$-

a_3a_3, would therefore become segregated. This cross provided the first clear-cut instance of transgressive segregation; it is illustrated by Baur (1914, pp. 144–146) from Nilsson-Ehle's specimens.

Nilsson-Ehle (1911) also explored the effects of multiple-gene systems on the inheritance of the length and density of the ears in wheat. The shape of the spikelike inflorescence of wheat is mainly controlled by the length of the internodes between the spikelets of the ear. The results from several crossings between distinct strains indicated that the genes controlling the length of the internodes of the ears were of two kinds, namely, lengthening genes, L_1 and L_2, which are found especially in the old so-called "land wheats," and a pair of shortening genes, CC, present especially in "compactum" types. The equilibrium between these genes working in opposite directions produces varied degrees of expression.

An illuminating example is the cross Swedish Binkelwheat, a compactum type, × Poodlewheat, a squarehead type (intermediate between compactum and the elongated ears of the land wheats). Neither of the parental strains was extreme in type of ears, but among the F_2 progeny were found types more condensed than the compactum parent, and others with more open inflorescences than those of the squarehead parent. The lengths of the internodes between the spikelets were measured in the parental strains, the F_2, and the F_3 progenies. A summary of the segregated phenotypes and the corresponding genotypes is presented in table 53.

The segregation in wheat for length of internodes of ears and for type of ears is the first well analyzed example in which the principle of transgressive segregation was clearly represented. Land wheat types having loose ears can be obtained from a cross between a dense-eared compactum and a fairly dense-eared squarehead, and strains that are more compact than compactum can likewise be obtained from the same cross.

Nilsson-Ehle used the *Triticum* example to illustrate that the gradual effect of the two lengthening genes, L_1 and L_2, could be completely covered by the epistatic effect of one dominant shortening gene, C. The variation becomes discontinuous if there is segregation for C; on the other hand, if C is removed, the L genes will provide variation in very small steps. He therefore demonstrated that the difference between qualitative and quantitative inheritance, and between discontinuous and continuous variation, is one of degree only.

TRANSGRESSIVE SEGREGATION IN NICOTIANA. The principle of transgressive segregation was soon confirmed by Hayes (1912) in a study on the inheritance of the number of leaves in crossings between distinct strains of tobacco, *Nicotiana tabacum* L. of the Solanaceae. The strains 405, Cuban, and 402, Havana, each having a mean number of 20 leaves, were crossed, and their F_1 had the same number as the parents. In the F_2, however, the number of leaves on the 193 plants obtained ranged between 14 and 23, indicating transgression in both a minus and a plus direction.

TABLE 53

INHERITANCE OF LENGTH OF INTERNODES BETWEEN SPIKELETS IN EARS OF WHEAT (AFTER H. NILSSON-EHLE, 1911)

Swedish Binkelwheat, $CCL_1L_1L_2L_2$ compactum type, not extreme, 1.9 mm. × Poodlewheat 0315, $ccl_1l_1l_2l_2$ squarehead type, 3.3 mm.

F_1: compactum type, $CcL_1l_1L_2l_2$

FREQUENCIES

F₂ PLANTS					F₃ PROGENIES	
	Phenotypes	Observed frequencies	Calculated frequencies	Genotypes	Kinds of segregation	Observed frequencies
66 compactum	supercompactum 1.4–1.6 mm.	2	1.5	$CCl_1l_1l_2l_2$	Constant supercompactum	2
	compactum 1.6–2.2 mm.	59	58.6	$C \cdot L \cdots$	Constant compactum	21
					Segregating noncompactum	38
	loose compactum	5	5.9	$CcL_1L_1L_2L_2$	Segregating noncompactum	5
28 noncompactum	squarehead 2.9–3.4 mm.	2	1.5	$ccl_1l_1l_2l_2$	Constant squarehead	2
	land wheat 3.4–3.9 mm.	24	20.0	$ccL \cdots$	Segregating from 3 to 5 mm.	24
	extreme land wheat 4.0–4.2 mm.	2	1.5	$ccL_1L_1L_2L_2$	Constant extreme land wheat	2
Total		94	94.0			94

Figures in millimeters indicate average distance between spikelets.
C (compactum): dominant, epistatic shortening gene.
L_1 and L_2: multiple, additive lengthening genes, hypostatic under C.

GENE SYSTEMS REGULATING QUANTITATIVE CHARACTERS IN MAIZE. Although Nilsson-Ehle's investigations of polymeric genes regulating various shades of grain color in oats and wheats introduced new concepts in genetic investigation, it was especially the investigations by East (1910) and by Emerson and East (1913) on *Zea mays* L. that proved the Mendelian case for characters having more or less continuous variation.

East (1910) reported on crossing fifteen varieties of maize having yellow endosperm with varieties having white endosperm, all of which segregated in the ratio 3 yellow to 1 white in the F_2. One variety with yellow endosperm, however, was used for pollinating a white variety which produced an F_1 yielding 159 medium yellow and 149 light yellow hybrid kernels, indicating that the pollen parent was heterozygous for yellow. When sown separately, the light yellow F_1 seeds segregated in the ratio 3:1, producing 3111 light yellow to 1098 nonyellow F_2 seeds. The medium yellow F_1 seeds, however, segregated in the proportion of 3207 dark to light yellow: 227 nonyellow, indicating a 15:1 ratio. This appears to be the first multiple-gene ratio reported in maize.

On the basis of this experimental evidence, East (1910) discussed also the inheritance in crossings between strains of maize differing in the number of seed rows per ear. One strain had a modal number of 8 rows, and another a mode of 20 rows per ear. The F_1 progeny tended to be intermediate in row number, and East was able to show that the parental types, together with many intermediates, could be segregated in the F_2. The variation therefore gave the impression of being continuous. As an actual example, Emerson and East (1913) developed a 16-rowed form from a cross between a 12-rowed and an 8-rowed form. In another cross between Tom Thumb popcorn with 12 rows and Missouri dent corn with 18 rows, F_3 families varied in their modes between 12 and 20 rows. The data indicated that the gene system governing the number of seed rows is more complex than was suggested by East's earlier theory assuming three pairs of multiple genes having additive effects only.

More information on the inheritance of number of seed rows in ears of maize was presented by Emerson and Smith (1950), who demonstrated through crossings between twelve inbred lines of 12-rowed maize that all these lines had different genotypes with respect to row number. In later generations selection was effective in both the minus and the plus direction, so that on the minus side by transgressive segregation 8-rowed strains could be selected, and on the plus side a 22-rowed strain could be produced. Strains with a high number of rows were obtained through multiple crossings (the polycross method). Such selection had no effect in inbred nonhybrid lines.

In the crossings between the twelve inbred 12-rowed lines, 76 of the 78 F_1's had significantly more rows per ear than the parents. In other crosses between six 8-rowed and thirteen 12-rowed strains, however, only 6 combinations differed significantly in row number from the mean of the parents, and 5 of these shifts were in a negative direction. Such a reduction in number of rows after

crossing suggests that inhibiting genes for row number ("minus modifiers") may be present besides genes having additive effects.

Emerson and East (1913) documented the quantitative inheritance of many other characters in maize, including length and diameter of ears, weight and breadth of seeds, height of plants, number of nodes per stalk, length of internodes, number of stalks per plant, and number of days required from planting to flowering. The shifts in modes of the F_3 families, and the general reduction in variability of the F_3's as compared with the variability in the F_2's, presented convincing evidence that these quantitative characteristics were regulated by genes similar to those that control qualitative characters.

Oppositional genes governing aleurone color. The existence of systems of genes having oppositional effect was soon found in Indian corn (East and Hayes, 1911; Emerson, 1912). A number of additional genes affecting aleurone color of maize have been found since the first discovery of the series (Emerson, Beadle, and Fraser, 1935).

East and Hayes (1911) studied the inheritance of aleurone color in a cross between a plant of the dwarf Tom Thumb popcorn, having white seeds, and a plant of Black Mexican sweet corn, having purple seeds caused by pigment in the aleurone cells. Although both parents bred true when not crossed, the hybrid seed in the F_1 ranged from dark to very light purple. The authors therefore suggested that some of the gametes of the white Tom Thumb parent possessed a dominant inhibiting gene controlling purple aleurone color that was missing in others. This assumption was confirmed by approximately 70 F_3 progenies. F_2 plants with light-colored seeds were able to segregate darker ones, and dark-colored plants could segregate progeny with light seeds, indicating that some genes tend to lighten seed color and others to darken it.

Emerson (1912) crossed Tom Thumb popcorn with California rice popcorn, both strains having white seeds. The F_1 was also white, but in the F_2 a sprinkling of red and purple grains appeared. The genic structure for this segregation, IiCcPrprRr, was presented as shown in table 54. On the genic background of the strains used in the Emerson experiment, the gene I is far more absolute in its inhibitory action than it is in the strains used by East and Hayes.

In a later paper, Emerson (1918) pointed out that there are three complementary pairs of basic genes for aleurone color, all of which must be present if the seeds are to be colored. It was found that certain crosses of colorless × colorless produced colored F_1 seeds, but that the F_2 segregated in the ratio of 27 colored to 37 colorless, a reversal of the classic *Lathyrus* segregation of 9 colored to 7 colorless. Among 25,289 F_2 seeds of the maize hybrid the observed segregation was 10,674 colored to 14,615 colorless (calculated frequencies, 10,668.8: 14,620.2). Colored F_2 individuals were shown to be of four kinds, namely, those that in F_3 segregated in the ratios of 27:37; 9:7; 3:1, and those that were constant. The third complementary gene necessary for aleurone color besides C and R was A, later shown to be the basic gene for plant color.

PLANT COLORS IN MAIZE. In an extensive investigation, Emerson (1921) found four pairs of genes, A, B, Pl, and R, that regulate plant colors in maize. The A and R genes also regulate aleurone colors. The A_1 gene has four alternates at its own chromosomal location and two complementary multiples, A_2 and A_3, in other chromosomes. The B gene exists in four alternates, and the R gene in six alternates (Emerson and Anderson, 1932; Emerson, Beadle, and Fraser, 1935).

Although the genic control for plant colors in maize is complex, the major control can be accounted for through the action of three genes, A, B, and Pl, as shown in table 55. The dominant gene A is the basic gene controlling development of anthocyanin and is also one of three complementary genes basic

TABLE 54

SEGREGATION OF SEED COLOR IN MAIZE (DATA FROM EMERSON, 1912)

Tom Thumb, IICCPrPrRR ———— × ———— California rice popcorn, iiccprprrr
white — white

F_1: white, IiCcPrprRr

F_2 FREQUENCIES

Aleurone color	Observed	Calculated	Ratio	Genotypes
White	530	538	220	I······ and all ii's that lack C, R, or both
Purple	75	66	27	iiC·Pr·R
Red	21	22	9	iiC·prprR
Totals	626	626	256	

C and R: complementary basic genes for aleurone color.
Pr: gene for purple aleurone color; prpr: gene for red color.
I: dominant epistatic inhibitor for aleurone color.

for aleurone color. By itself and in the presence of light, the A gene produces a dilute red color (dilute sun red) in the stems and leaves, whereas its recessive alternate, aa, is green. The Pl gene induces purplish plant color. By itself, and in both light and darkness, it occasionally can produce a slight purplish tinge, but normally it requires the presence of either the A or the B gene, or both, for its expression. The B gene by itself and in light can induce slight brown coloring, but its main effect is to intensify dilute sun red of A to sun red, the trace of purple of Pl to brown, and the dilute purple of APl to purple.

The interaction among the A, B, and Pl genes resembles that of complementary genes in that they enhance the effects of one another; however, unlike true complementary genes, each produces a slight effect by itself, but this effect is intensified by the other genes. This system is a transition between one composed of complementary genes and one of genes having a cumulative effect.

A fine balance exists between the expression of the A, B, and Pl system of genes and certain kinds of environment (Emerson, 1921). One of the environ-

mental factors influencing the expression is light. The colors controlled by A and B develop only in light, not in darkness (table 55), but the presence of the dominant Pl gene enables the A and B colors to develop also when light is excluded.

Emerson (1921) found also that the phenotypic expression of the biotypes is influenced by the fertility of the soil. One lot of the various biotypes for plant color was grown in a rich mixture of equal amounts of field soil and well decayed stable manure, and another lot in a poor mixture of equal amounts of field soil and sand. The aa and A biotypes (table 55) could be distinguished

TABLE 55

Inheritance of plant colors of maize. Ratios of genotypes and of phenotypes in sunlight and in darkness in progeny of the heterozygote AaBbPlpl. (After Emerson, 1921.)

Genotypes	Phenotypes		
	In sunlight	In darkness	Ratio
27 ABPl	purple	purple	27
9 ABplpl	sun red	green	9
9 AbbPl	dilute purple	dilute purple	9
3 Abbplpl	dilute sun red	green	3
9 aaBPl	brown	brown	9
3 aaBplpl	slightly brown	green	3
3 aabbPl	trace of purplish	trace of purplish	3
1 aabbplpl	green	green	1
Total			64

A: basic gene for anthocyanin coloration; by itself and in light it produces dilute sun red color.
B: intensifier for color; by itself and in light it produces slightly brown color; it changes dilute red to red, dilute purple to purple, and trace of purplish to brown.
Pl: gene for purplish color; by itself it produces occasional traces of purplish tinge, but develops in both sunlight and darkness, and enables the A and B colors to develop even in darkness.

from each other much earlier in the poor than in the rich soil. However, the lighter and darker colors within the A series, ranging from dilute sun red to purple, were all so strongly developed in the unfertilized soil that they could not be distinguished from each other, although they could easily be distinguished in the fertilized soil. Similar responses were also observed in quartz sand cultures to which varying amounts of nutrient solutions were added.

Maize growing under field conditions in waterlogged soils was often observed to develop brilliant colors. On the basis of experiments with pot cultures supplied with varying amounts of water and exposed to different temperatures, Emerson (1921) concluded that the brilliant colors of maize in wet field soil were not produced directly by either the moisture or the cool temperature of the soil, but by the inability of the plants to absorb adequate supplies of nitrate

and phosphate. In this connection Emerson called attention to a paper by Czartowski (1914) on experiments with *Tradescantia* in which that author observed that plants developed strong color when supplied with a nitrogen-free solution, whereas anthocyanin gradually decreased in branches growing in solutions containing nitrogen. Czartowski suggested that deficiency in nitrogen inhibits protein synthesis, thereby releasing an excess of carbohydrates. Coloration due to anthocyanins is intensified as sugar content increases, since anthocyanins are composed of one or two molecules of sugar combined with one of the anthocyanidins.

In this connection Emerson (1921) pointed to the chain of events, starting with the necessary genic constitution, through the environmental effects on physiological and biochemical processes, that effect the expression of anthocyanin coloration in leaves. He expressed the hope "that some day thru the coordinated efforts of biochemists, physiologists, and geneticists, it may be possible to reach conclusions in this field of quite as fundamental importance to biology as the recent results of similar efforts of cytologists and geneticists."

Genes inhibiting the development of stripes in the shell of snails. In a genetic investigation of a land snail, *Tachea nemoralis,* Arnold Lang (1914) found that the basic recessive biotype for three pairs of genes, aabbcc, has five horizontal stripes on its shell, the highest number that any snail of this species possesses. When the dominant gene C is added to the biotype, aabbC, stripes 1 and 2 from the top are removed, so that only stripes 3 to 5 remain. Gene B removes all stripes except number 3, and B is epistatic over gene C. Finally, gene A inhibits all five stripes and is epistatic over both B and C. The operation of these three multiples of subtractive effect is shown in table 56, which lists the ratio of genotypes and phenotypes segregated in the progeny of the heterozygote AaBbCc.

The highly specific effect of the individual genes listed in table 56 combined with a strictly epistatic system determines the phenotypic variation seen in this snail. Starting with the top epistatic unadorned AABBCC type, a series of three recessive mutations makes possible the extensive variation now observed. The b and c mutations, however, could not come to expression before the mutation of A to a had occurred. Another consideration is that, in analogy with the situation in other organisms, the unanalyzed part of the *Tachea* biotype probably contains positive genes controlling the development of the shell stripes that are removed by the inhibitors C, B, and A.

Shape of leaves and capsules in Capsella. One of the first to demonstrate that Mendelian principles control characters used by taxonomists was G. H. Shull, through his classic investigations on the genus *Capsella,* the shepherd's-purse. Following the American code of nomenclature, Shull listed the genus as *Bursa.*

In 1909 Shull reported on the existence of several elementary species in the

sense in which H. de Vries applied the term (1901). These occurred within the Linnaean species *Capsella bursa-pastoris* (L.) Moench. of the Cruciferae, a species which Linnaeus referred to the genus *Thlaspi.* Shull obtained the seeds of these elementary species now known as biotypes from various localities in North America and in Europe, where the species grows as a weed in cultivated areas.

Shull distinguished four major types among his very extensive collections, according to the shape of the leaves of the basal rosette. These were *simplex,* having fairly obtusely lobed leaves; *tenuis,* having leaves with narrow, almost flagellate, lobes and, like *simplex,* not dissected to the midrib; *rhomboidea,* having leaves dissected to the midrib but with broad, rounded lobes; and *heteris,* dissected to the midrib but having lobes that are rounded at the base of the lobe as in *rhomboidea,* and ending in a sharply differentiated, almost flagellate tip,

TABLE 56

INHERITANCE OF DOMINANT, EPISTATIC INHIBITORS OF STRIPES ON THE SHELLS OF THE SNAIL TACHEA NEMORALIS. RATIO OF GENOTYPES AND PHENOTYPES IN PROGENY FROM THE HETEROZYGOTE AaBbCc. (AFTER ARNOLD LANG, 1914.)

Genotypes	Stripes developed	Ratio
A·····	None	48
aaB···	No. 3 stripe only	12
aabbC·	Nos. 3, 4, and 5 only	3
aabbcc	All five	1
Total		64

A: epistatic inhibitor of all five stripes.
B: inhibitor of stripes 1, 2, 4, and 5 computing from the top; hypostatic under A, but epistatic over C.
C: inhibitor of stripes 1 and 2 from the top; hypostatic under A and B.
The triple recessive has all five stripes.

as in *tenuis.* Some of the strains were constant for these characters, but others were heterozygous and segregated after self-pollination.

Some forms of *heteris* were constant, but others segregated in a two-gene ratio of approximately 9 *heteris* to 3 *rhomboidea* to 3 *tenuis* to 1 *simplex,* or in one-gene ratios of 3 *heteris* to 1 *simplex,* or 3 *heteris* to 1 *rhomboidea.* The *rhomboidea* form could either be constant, or segregate into 3 *rhomboidea* to 1 *simplex,* and likewise the *tenuis* form could be constant, or segregate the *simplex* form.

These data indicated that a simple gene system controls the shape and lobing of the rosette leaves in *Capsella.* The operation of the system can be seen from table 57. The *simplex* form is the double recessive, aabb, and has round lobes; the addition of an A gene, Abb, narrows the lobe to *tenuis;* both these bb forms, however, are lobed only and not cut to the midrib. The addition of the B gene, aaB, dissects the leaf to the midrib, and the B gene produces also round lobes, *rhomboidea.* When the A and B genes are combined into the double dominant *heteris* biotype, AB, the effects of the two genes are added so that *heteris*

has the deep cut and round base of the lobe produced by the B gene in addition to the narrow lobe tip controlled by the A gene.

In a later paper Shull (1929*a*) showed that another gene, I, is responsible for the initial lobing of the *simplex* form. In some of his crossings Shull used a form of *Capsella* that had shallowly sinuate rosette leaves. This form had been collected in Wales near Penarth and at Cardiff, and Shull described it as *Bursa penarthae.* In crossings between *penarthae* and other forms of *Capsella,* a fairly

TABLE 57

INHERITANCE OF CAPSULE SHAPE AND LEAF SHAPE IN CAPSELLA. FREQUENCIES OF PHENOTYPES AND GENOTYPES IN F_2. (AFTER SHULL, 1909.)

C. heegeri heteris ——×—— *C. bursa-pastoris simplex*
AABBccdd aabbCCDD
F_1: AaBbCcDd

F_2 FREQUENCIES

Leaf shape	Capsule shape: *bursa-pastoris* CD, Cdd, and ccD	Capsule shape: *heegeri* ccdd	Total	Calculated	Ratio
heteris, AB	1447	69	1516	1428.8	9
rhomboidea, aaB	401	19	420	476.2	3
tenuis, Abb	469	21	490	476.2	3
simplex, aabb	112	2	114	158.8	1
Total	2429	111	2540	2540.0	16
Calculated	2381.2	158.8	2540.0		
Ratio	15	1	16		

A: gene narrowing lobes of rosette leaf.
B: gene dissecting leaf to the midrib, and rounding the leaf sector.
aabb: recessive, having round-lobed rosette leaves.
C and D: multiple, dominant genes for triangular capsule.
ccdd: recessive, having ellipsoid capsule.

basic recessive eventually appeared having entire leaves, a form Shull named *simplissima.*

When the entire-leaved *simplissima* was crossed with the round-lobed *simplex,* a *rhomboidea* F_1 resulted having deeply dissected leaves and rounded lobes. Shull explained this transgressive result by assuming that the synthetic entire-leaved *simplissima* had the genetic formula aaBBii, so that it possessed the B gene for rhomboidly dissected leaves in addition to a recessive inhibitor for lobing. It would be simpler to assume that the *simplex* parent possessed a basic gene, I, for incision in leaves, having the formula aabbII, and that the entire-leaved *simplissima* lacked the incision gene although it possessed the B. In accord with this theory, the cross aaBBii, *simplissima,* × aabbII, *simplex,* re-

sulted in a deeply incised F_1 having the formula aaBbIi. This F_1 was deeply incised because it possessed the I gene, and was rhomboid because of the gene B. According to the latter assumptions, all the 1909 crossings were homozygous for I.

Capsella penarthae itself had shallowly sinuate leaves, a leaf form not accounted for by any one of the genes A, B, or I, alone or in combination. It is therefore evident that at least four pairs of genes control leaf shape in *Capsella*. Some of Shull's data would suggest that even more genes may be responsible for other modifications in leaf form.

Another series of Shull's studies on *Capsella* dealt with an intraspecific difference of the seed capsule comparable to differences that exist between certain genera of the Cruciferae. In 1897 Professor G. Heeger discovered at the market-place of Lindau, Germany, a few plants of a species that did not fit the description of any known species. They occurred in the center of a large colony of *Capsella bursa-pastoris*. Count Solms-Laubach and Dr. Ascherson, who were shown the specimens (Solms-Laubach, 1900), were at first inclined to refer them to the neighboring genus *Camelina* because of the ellipsoid capsules. Cultures grown from seeds of the new species segregated some progeny that developed the capsule form of *Capsella bursa-pastoris*. This observation was made before the year 1900, and the *bursa-pastoris* plants were called "atavistic reversions," although they probably resulted from outcrossing between the new species and surrounding plants of *C. bursa-pastoris*.

The new form was given the name *Capsella heegeri* Solms, after its discoverer. Because the region was botanically well known, the appearance of the new species was widely heralded and interpreted as being an authentic case of the origin of a new species by saltation or mutation (de Vries, 1901). Shortly after its discovery, however, the new *C. heegeri* disappeared from its only known habitat (Shull, 1910), although it has been maintained under cultivation in botanical gardens.

Shull crossed *Capsella bursa-pastoris simplex* with *C. heegeri heteris*. In both directions the F_1 progeny showed complete dominance of the *bursa-pastoris* type of capsule and the *heegeri* type of leaf. In the F_2 a segregation concerning shape of capsule took place that approached a ratio of 15 *bursa-pastoris* to 1 *heegeri,* as is shown in table 57 (Shull, 1909). These data were first communicated at the 7th International Zoological Congress at Boston in 1907 (Shull, 1910), and such a ratio was unknown at the time, inasmuch as this communication preceded Nilsson-Ehle's classic investigations on polymeric genes. In 1914, however, Shull identified the segregation in *Capsella* capsules with polymeric genes. This conclusion was fortified by the evidence that in the F_3 and F_4 some families segregated in the ratio 3:1, others continued in the ratio 15:1, and some became constant.

Shull (1914) suggested that the numerical deficiency in F_2 plants having *heegeri* capsules (table 57) might be due to losses because of weakness of the double recessive *heegeri*. In F_3 progenies, however, families with 3:1 ratios showed no

noticeable deficiency in *heegeri.* A more likely explanation is that the aberrant ratio in the proportion of F_2 plants having *heegeri* capsules resulted from a mixture of allo- and autosyndetic pairing among the chromosomes of the F_1 hybrid. *Capsella bursa-pastoris,* including *C. heegeri,* is a tetraploid species having 16 pairs of chromosomes as compared with 8 pairs in diploid but closely related species of the genus. The ratio of a two-gene segregation in the tetraploid species would be 35:1 if there was completely random autosyndetic pairing of either *heegeri* with *heegeri, heegeri* with *bursa-pastoris,* or *bursa-pastoris* with *bursa-pastoris* chromosomes, and it would be 15:1 if the pairing was completely allosyndetic. The observed ratio in the hybrid was intermediate between these two, 23:1. It should be emphasized that the chromosome numbers of the plants were not known to Shull at the time of this experiment; in fact, the concept of polyploidy was not developed until several years later.

The shape of the capsule of *Capsella* is apparently governed by a system of two multiple genes, C and D, that regulate the growth processes that eventually determine the difference between the triangular and ellipsoid capsules of these two entities. The presence of just one of these dominant genes is apparently sufficient to change the *heegeri* capsule to the type of *bursa-pastoris.*

Other genes that affect the capsule shape may, however, also be present, inasmuch as Shull (1929*a,* p. 847) mentioned that *heegeri* can give rise to a transitional form called *solmsiana* which has a triangular capsule but without the incision at the top found in *bursa-pastoris.* Shull observed that in the course of many generations in one botanical garden near Berlin the *heegeri* form had changed to *solmsiana,* although it had not reverted to the *bursa-pastoris* type as did the original population at Lindau. Unlike *heegeri* and *bursa-pastoris, solmsiana* is modifiable, because in certain plants the capsules near the top of the raceme are of the *solmsiana* type, whereas at the base they may be of the *heegeri* type. This unstable expression suggests a close balance between positive genes and inhibitors.

It is of interest that in a large number of crossings between wild *bursa-pastoris* from North America and Europe with *heegeri* the hybrids segregated in the approximate proportion 15:1. Only two exceptions were found. One was a strain of *bursa-pastoris* from Lindau, Germany, the original habitat of the *heegeri* form (Shull, 1929*a,* p. 842), and the other was a strain from near Uppsala, Sweden (Dahlgren, 1915). It is highly suggestive that one of the strains of *bursa-pastoris* with unduplicated genes for triangular capsule came from the population in which the original *heegeri* "mutant" originated. Apparently the potentiality for occurrence of this form lay in the gene frequency of the CD series in the Lindau population. Genes for ellipsoid capsule may have existed in a past geologic period when the genera *Capsella* and *Camelina* evolved from a common ancestor.

According to our present concepts, *Capsella bursa-pastoris* and *C. heegeri* belong to the same biological species even though their morphological differences suggest different genera according to taxonomic criteria used in the Cruciferae.

Inheritance of leaf shape and stellate pubescence in Camelina. It is of interest that the flaxweed, *Camelina sativa* (L.) Crantz, of the Cruciferae, a species having 20 pairs of chromosomes, has a genetic basis governing leaf shape that somewhat parallels the one found in the related genus *Capsella* just discussed. Tedin (1923, 1925) analyzed genetically the 6 F_2's resulting from polygonic (diallel) crossings among four parental strains of *Camelina sativa* together with 603 F_3 progenies. As a result of this extensive analysis he found that an entire-leaved form, *integrifolia,* was double recessive, aabb. In *Camelina* the addition of a B gene, aaB·, produces shallowly sinuate dentation similar to the dentation in Shull's *Capsella penarthae,* a leaf form to which no corresponding formula was assigned in Shull's experiments. The addition of A and B genes, AB, produces leaves that are deeply dissected to the midrib. In all combinations the homozygotic dominant is a little more distinct than the heterozygote. There is a noticeable similarity in the basic genetic control of leaf shape in *Camelina* and *Capsella.* In *Capsella,* however, the effects of the A and B genes are more specific than in *Camelina,* the genes of which have more of an additive effect.

The stellate pubescence on the leaves of *Camelina* was found to be controlled by a system of at least three pairs of dominant genes, D_1 to D_3. In crossings between three forms of flaxweed having stellate pubescence and a strain having almost smooth leaves, hairy was found to be dominant over smooth. Pubescent *Camelina sativa linicola foetida* × smooth *C. s. linicola integrifolia* segregated in the F_2 in the ratio 3 pubescent to 1 smooth, indicating the genetic formula $D_1D_1d_2d_2d_3d_3$ for the pubescent parent. With *C. s. linicola macrocarpa* as the pubescent parent, the F_2 segregation was in the ratio 15 pubescent to 1 smooth; with *C. s. ruderalis,* 63:1, in a population of 2555 individuals. The last ratio would indicate that this strain of pubescent *ruderalis* had the genetic formula $D_1D_1D_2D_2D_3D_3$. A triangle of crossings among the three stellately pubescent parental strains produced no smooth F_2 plants in cultures consisting of 543, 2343, and 5064 plants. The absence of smooth plants indicates that the three pubescent *C. sativa* strains had at least the D_1D_1 pair of genes in common.

Multiple genes in diploid Crepis. When the principles of duplicated genes, duplicated chromosomes, and polyploidy were discovered, it was generally assumed that diploids should segregate in monogenic ratios, and polyploids in polymeric ratios. It does not follow, however, that diploids cannot possess systems of multiple genes. Genetic experiments on diploids soon indicated that polymeric ratios were common within such species, although this fact even today has not become thoroughly assimilated in current genetic theory.

The extensive studies of E. B. Babcock and his associates (Babcock, 1947) brought to light many multiple-gene segregations in species of the genus *Crepis* of the Compositae, which are characterized by low numbers of chromosomes. The first clear evidence of the occurrence of multiple genes in a diploid species was found in *Crepis capillaris* L., which has only 3 pairs of chromosomes, the lowest known number among the phanerogams. Several duplicate sets of genes

were found by J. L. Collins (1924) in a genetic analysis of nearly a score of morphological characters in this species. One of these included duplicate inhibitors for hairs on the midrib of the leaves segregating in the proportion 743 smooth to 49 hairy. In *Camelina* the nonhairy form is the recessive phenotype, but in *Crepis capillaris* it is a double dominant. Another character in *Crepis capillaris* having multigenic control is flat as compared with revolute leaves. The segregation for this character was 233 flat to 20 revolute, indicating that a minimum of two pairs of dominant genes ensure the development of the normal flat leaf.

Crepis capillaris was also found to possess characters controlled by systems of complementary genes, producing segregations in the ratio 9:7. Anthocyanin coloration yielded a segregation of 166 anthocyanous to 109 nonanthocyanous plants, and leaf lobing segregated 142 plants having angular leaf lobes to 112 having round lobes (J. L. Collins, 1924).

Babcock and Cave (1938) studied the genetic factors controlling some of the characters that distinguish subspecific entities of the diploid 4-chromosome *Crepis foetida* L. complex. *Crepis foetida commutata* Spr. has flat, elongate scales (paleae) on the receptacle of the head. The paleae are replaced by long hairs in all other subspecies of *foetida*. In crossings between the paleate *C. foetida commutata,* from the island of Lesbos, and forms of *Crepis foetida vulgaris* Bisch., having hairy receptacles, from Syria and the island of Cyprus, the F_1 was paleate. The F_2's segregated according to the ratio 51 paleate to 13 hairy, as is indicated in table 58. This ratio suggests that three pairs of genes are involved, and that *commutata* has two pairs of dominant multiple genes governing the development of paleae, *vulgaris* being recessive for both; on the other hand, *vulgaris* possesses a dominant inhibitor for one of the palea genes, but this inhibitor does not influence the other palea gene.

In F_2's between other crossings of the subspecies *commutata* and the subspecies *vulgaris, eritreënsis* Babc., and *thompsonii* Babc., 15:1 or 63:1 segregations appeared to take place for paleate as compared with hairy receptacles, indicating that in the various forms of *Crepis foetida* this difference is controlled by a series of three to four genes, although in other groups of Compositae this character may denote generic or tribal distinctness.

The inheritance of ligule color in the *Crepis foetida* complex parallels the inheritance of petal color in *Potentilla glandulosa,* except that in *Crepis foetida* no dominant white was found. Babcock and Cave reported (1938) that *Crepis foetida* had chrome, *C. eritreënsis* lemon yellow, and *C. thompsonii* "cream" ligules (the last probably comparable to the extreme recessive "pale yellow" in *Potentilla*). In the *Crepis foetida* complex an epistatic series of genes for color apparently exists, inasmuch as lemon yellow was found to be epistatic over cream, and chrome over lemon, so that segregations of 12:3:1 occurred. Because chrome and lemon were merged into one class, this type of segregation was tabulated as being 15:1. The cross between the lemon *eritreënsis* and the cream *thompsonii* segregated in the ratio 3 lemon to 1 cream (78:23); that of *thomp-*

sonii × *foetida* in the ratio 15 chrome + yellow to 1 "cream" (127:10); whereas *eritreënsis* × *foetida* segregated also in the ratio 15 chrome + yellow to 1 "cream" (173:19). The results from this triangle of crossings indicate, therefore, that, if cream *thompsonii* is double recessive, xxyy, the lemon yellow *eritreensis* is xxYY, and the chrome *foetida* is XXyy. In this series the Y gene controls the development of lemon yellow color, and the X gene the development of the epistatic chrome color.

Five taxonomic entities of the complex of *Crepis vesicaria* L., all having 4 pairs of chromosomes, occupy geographically separated habitats on the Atlantic islands of North Africa. Jenkins (1939) investigated the genetic relations of all

TABLE 58

INHERITANCE OF PALEATE VERSUS HAIRY RECEPTACLE IN CROSSES BETWEEN SUBSPECIES OF CREPIS FOETIDA (AFTER BABCOCK AND CAVE, 1938)

C. foetida commutata ——×—— *C. foetida vulgaris*
paleate, RRSSii hairy, rrssII
F_1: paleate, RrSsIi

F_2 FREQUENCIES

Phenotypes	Genotypes	Observed	Calculated	Ratio
Paleate	48 R····· / 3 rrSii	202	195.8	51
Hairy	9 rrSI / 4 rrss··	44	50.2	13
Total		246	246.0	64

R and S: dominant multiple genes for development of paleae on receptacle; S, but not R, can be suppressed by an inhibitor, I.
I: dominant inhibitor for S.
rrssii: recessive background genotype producing hairy receptacle.

five: *Crepis vesicaria taraxacifolia* (Thuill.) Tell., an annual weedy form on the south side of the island of Madeira; *C. vesicaria andryaloides* (Lowe) Babc., occurring on steep cliffs and mountain sides on the north side of the island; *C. divaricata* (Lowe) Shultz, from a detached promontory on the east side of Madeira; *C. noronhae* Babc., from the island of Porto Santo, near Madeira; and *C. canariensis* (Sch. Bip.) Babc., from the Canary Islands. All except the first are perennial to biennial and probably have been on the islands for a long time; *taraxacifolia* apparently has been introduced fairly recently from Portugal (Babcock, 1947).

The five entities of the *Crepis vesicaria* complex are morphologically distinguishable, although they obviously are rather closely related. They cross easily; their chromosomes are morphologically alike and pair normally; and the F_1 hybrids are fertile, although a little less so than the parental entities. There is a fairly distinct genetic barrier between *divaricata* and *canariensis,* but

indirectly these species can be linked through hybrids with other species. The segregation for each of seven character differences investigated in the hybrid *C. divaricata* × *C. vesicaria taraxacifolia* was distinctly of a quantitative kind controlled by multiple genes. Even in F_2 progenies as small as 125 plants some tendency for transgressive segregation was observed. Studies on F_3 derivatives are lacking, but the position of the parental forms and the F_1's in relation to the F_2 frequency curves suggests that some of the multiple genes that regulate the differences among these ecologically closely related entities are not of the simple additive kind.

The *Crepis foetida* and *Crepis vesicaria* complexes thus both contain spatially isolated population complexes that are morphologically distinct and have been named as taxonomic species, but they have not evolved barriers to interbreeding. In certain respects they resemble the *Potentilla glandulosa* complex, but in *Potentilla* the crossings were made between environmentally contrasting ecological races, whereas in the *Crepis vesicaria* complex hybrids were made between spatially isolated populations within the same ecological zone.

Multiple genes governing seed size in peas. The common pea, *Pisum sativum* L., was the object of Mendel's classic investigations involving genes of major morphological effect. Nevertheless, this diploid 7-chromosome species also has genes of the multiple type. One series of investigations on seed weight by Winge (1936) is especially illuminating, because some of the multiple genes that affect seed weight can be identified.

In crossings between "Rosa" and "Lolland raisins," the latter strain had a seed weight of about 56 cg., and the former a weight of only 17 cg. The weight of the F_1 was below the mean of the parents. No transgressive segregation was observed in the F_2, consisting of 619 plants. Of the various morphological characters that segregated in this F_2, only one, yellow as contrasted with green seed color, showed correlation with seed size. In peas, seed color is the color of the cotyledons of the embryonic seedling which fills the entire space within the seed coat. It is therefore not a characteristic of the plant that bears the seed, but of the next generation. The yellow seed color was introduced by the large-seeded parent. In the F_2 the mean seed weight of the homozygous yellow-seeded plants was 3.21 ± 0.69 cg. higher than that of the recessive green-seeded plants.

These findings were supported by those of another cross, "Light violet spotted" × "Unmarbled Lolland raisins," in which the seed weights of the parental strains were similar to those of the preceding cross, and large weight was also introduced by the yellow-seeded parent. The weight of the F_1 was again below the mean weight of the parental strains, suggesting the prevalence of genes of inhibitory effect on seed size. In an F_2 consisting of 1506 plants there was no transgressive segregation, but again the homozygous yellow-seeded F_2 plants had a higher seed weight than the recessive green-seeded plants, the difference being 1.30 ± 0.41 cg., which is statistically significant. The correla-

tion between large seed weight and yellow seed color suggests that one of the genes contributing to high seed weight is located in the chromosome carrying the single gene for yellow seed color.

In contrast, in the cross "Stolz des Marktes" × "Falcate" high seed weight was associated with green seed color. High seed weight was introduced by "Stolz des Marktes," which has green seeds and short nodes. The seed weights of the parents were approximately 44 and 21 cg., respectively, but the weight of the F_1 was higher than the mean of the parental strains, suggesting the prevalence of genes of positive effect. There was, moreover, transgressive segregation in the F_2, consisting of 1825 plants, the seed weights varying between 13 and 51 cg. In this F_2 the mean seed weight of the recessive green-seeded plants was 2.01 ± 0.42 cg. higher than that of the homozygous yellow-seeded plants. Because in certain crossings high seed weight is associated with yellow seeds, and in other crossings with green seeds, it seems evident that one of the genes affecting seed size is located in the same chromosome that contains the gene determining yellow as contrasted with green seed color, but that it is not identical with that gene.

The cross "Stolz des Marktes" × "Falcate" also yielded segregating F_2 progeny with respect to length of internodes. In the F_2, plants having long internodes had seeds that on the average were 3.73 ± 0.43 cg. heavier than seeds of plants having short internodes. The gene for long internodes is therefore correlated with larger seed weight, although it was introduced by the small-seeded "Falcate" parent. The chromosome that carries the gene for long internodes therefore also carries a gene for increase of seed weight, but this chromosome is not the same as the one that carries the gene for yellow seed color.

A third gene governing seed size in peas is apparently located in a linkage group containing the gene Pl for black placenta. In the cross "Violet spotted" × "Unmarbled Lolland raisins" the seed weights of the parents were 19 and 56 cg., respectively. The weight of the F_1 was again below the mean weight of the parental strains, and there was no obvious transgressive segregation among a population of 1354 F_2 plants. The seeds of the small-seeded parent had black placentae, and those of the large-seeded parent uncolored placentae. In the F_2, plants having the recessive uncolored placentae had seeds that on the average were 1.87 ± 0.42 cg. heavier than seeds of plants having black placentae. In two other crossings, however, there was no significant difference in seed weight between F_2 plants having black and F_2 plants having uncolored placentae. It was therefore concluded that the correlation between large seeds and uncolored placenta of the first cross represented genetic linkage, and not a pleiotropic effect of the placenta gene. It is more likely that the correlation was produced by a gene that reduces seed size, which would be carried by the small-seeded "Violet spotted" parent having black placentae.

Another cross of *Pisum* resulting in highly transgressive segregation of seed weight is of special interest because the differences were associated with a combination of genes regulating flower color rather than with a single gene. In the

cross "Light purple" × "Beauty," the two parental strains had seed weights of about 32 and 43 cg., respectively. The weight of the F_1 was considerably less than the mean of the parental weights. The F_2 population consisted of 378 plants, and its mean seed weight corresponded to the mean weight of the parents. The segregation for seed weight in the F_2 was highly transgressive, however, ranging between 13 and 57 cg.

Three pairs of genes controlling flower color segregated in this cross. Five phenotypes of flower color were observed, namely: purple, AArB; rose, AArbb; violet, AararB; light purple, Aararbb; and white, aa····. The plants having violet flower color, AararB, had also distinctly smaller seed weights than plants having other flower colors. Violet-flowered plants ranged from 9.25 ± 3.37 cg. to 14.41 ± 1.61 cg. less in seed weight than seeds of rose- and purple-flowered plants, respectively, the light purple and white types being in between. This seed-weight-reducing effect of the AararB biotype is apparently pleiotropic, and is produced only by that particular gene combination. Another pleiotropic effect associated with violet-flowered plants is that their seeds have abnormally contracted placentae, so that food transport from the mother plant to its seeds is impaired.

Four different genes and gene combinations governing morphological characters were therefore found to be correlated with genes controlling seed weight in peas. On the other hand, other morphological characters, such as mottled seeds, violet seed dots, and colored leaf axils, showed no correlation with seed weight. The results provide convincing evidence that several genes of a multigenic system governing seed weight can be heritably associated with others that control several unrelated morphological characters.

Genes controlling pod shape in peas. An intricate system of genes controlling the development of shape and texture of the pod of the pea has been discovered in this classic object for genetic study. The interaction of about eight pairs of genes that regulate the development of seed pods in *Pisum* can be traced in a series of studies by Wellensiek (1925*a,* 1925*b*), Nilsson (1929), and Lamprecht (1936, 1938, 1953). These genes and their effects are summarized in table 59.

Disregarding the historic and devious sequences by which the concept of these gene actions gradually unfolded, it can be stated that some pea strains have straight pods, others concave pods (having seeds along the concavely curved midrib of the carpel), and still others convex pods (seeds attached to the convex midrib). Very young pods of all strains are convexly curved. Mature pods will remain convex in those strains in which the ratio of growth increments along the two edges of the pod (the midrib and the edges of the carpel) remains unchanged during development. In other genetic types, however, the pod begins to grow moderately faster along the midrib than along the edges, resulting in a straight mature pod. With other combinations of genes, the growth rate

along the midrib is accelerated so much over that along the margin that the pod which was originally convex becomes strongly concave when mature.

When homozygous, the recessive gene cp (table 59) tends to curve the pods concavely, whereas its dominant counterpart, Cp, tends to straighten them. The Cp gene accelerates the growth along the midrib more than the cp gene. In contrast, there are two pairs of multiple genes, con and co, which in homozygous condition tend to hold the pod to the convex shape. Their two dominant counterparts, Con and Co, however, tend to straighten the pod in a manner similar to the Cp gene. All the dominant genes in this series, therefore, tend to straighten the pods as compared with their recessive counterparts. Despite this similarity in expression of these genes, they are opposite in their physiological action. The Cp gene accelerates growth along the midrib of the carpel, whereas the Con and Co genes retard growth as compared with the recessive con and co genes.

TABLE 59

SUMMARY OF GENES CONTROLLING CHARACTER OF PODS IN CULTIVATED PEAS

1. *Genes controlling curving of pod*

Cp: produces straight pods; cp: concavely curved pods
Con and Co: multiples producing straight or concavely curved pods
con and co: convex pods
N: (1) straightens or convexes pods from the concave or straight shape, respectively
(2) produces pod wall of normal thickness
(3) produces square ends of pods
(4) lengthens pod
n: (1) curves pods concavely irrespective of whether the plant is Cp or cp
(2) produces a pod wall that is 2 to 3 times as thick as in normal plants
(3) tapers both ends of the pods irrespective of the presence of Bt for blunt pods
(4) shortens pod
nnConCon: concavely curved
nnconcon: straight pods (the oppositional effects of n and con neutralize each other)
NNconcon: convexly curved
NConCon: straight

2. *Gene combinations controlling pod membrane*

ppvv: no membrane
Pvv: thin inner membrane in pod
ppV: strong strip of membrane along midnerve of pod only
PV: normal membrane (complementary effect of two genes)

3. *Genes controlling pod length*

Le: produces long pod (N also lengthens the pod)
le: shortens pod (n also shortens the pod)

4. *Genes controlling pod tip*

Bt: produces blunt tip of pod (N also produces blunt pod)
bt: tapers tip of pod (n tapers both ends of pod)

A fourth recessive gene, n, when homozygous will also tend to curve the pod toward concave (table 59), whereas its normal dominant counterpart, N, tends to straighten the pod or even to make it convex, depending upon which other genes of the series may be present. The n gene is drastic in its effects, for besides curving the pod it causes the walls of the pod to become two or three times as thick as in plants carrying the gene N. The n gene also tapers both ends of the pod.

This complex system of genes was not discovered until Lamprecht used a rare old strain in his crossings, Vilmorin's "Pois Sabre," the only strain of peas known to have a convex pod. Until that time only a one-gene difference, Cp-cp, was known. Complex gene situations such as the one described for pod curvature have led to conflicting statements about the genetic linkage of this character. Curved pods may show a correlation with one character in one cross, but not in other crosses where it might be correlated with another character controlled by a gene in a different chromosome. Such a situation can be expected in the inheritance of a character for which there is multigenic control.

Table 59 lists also genes affecting other characters of the pod on the basis of Lamprecht's studies cited above. The membrane that lines the inside of the pod is regulated by two complementary genes, P and V. When both these genes segregate, the ratio of plants having normal membrane to those having deficient membrane is 9:7. The length of the pod is controlled by one pair of genes, and the shape of its tip by another pair. In addition to their aid in curving the pod and controlling the thickness of its wall, the N and n genes also influence the length of the pod and the shape of its tip. The eight pairs of genes that control the development of the pods thus form an integrated genetic system.

Lamprecht (1953) lists eight other pairs of genes in the 7-chromosome peas that are multiple or complementary. An example of complementary genes is the pair Br and Bra, both of which are required for the development of bracteoles. A cross between two parent strains neither having bracteoles produced an F_1 hybrid having small bracteoles, and an F_2 of 466 plants, of which 252 had short to long bracteoles and 214 had none. One bractless parent of this cross was brbrBraBra; the other, BrBrbrabra. The F_1, accordingly, was BrbrBrabra. The genes BrBr and BraBra have no effect by themselves, but the double dominant BrBrBraBra has longer bracteoles than the heterozygous F_1. This system of genes is an example of both complementary and cumulative effect. The two kinds of genes are complementary, and both are needed to cause activation. If, however, both kinds are present in heterozygous condition, the addition of an extra Br or Bra gene enhances the effect.

It is noteworthy that an old cultivated crop plant, such as the pea, can have gene systems similar to systems that regulate morphological characters of wild plants. In many cultivated plants the dominant and epistatic inhibitors and modifiers of gene systems have been lost through man's selection.

Genes of oppositional effect controlling fruit shape in Cucurbita. The squashes belonging to the species *Cucurbita pepo* L. have 20 pairs of chromosomes and contain cultivated races having highly contrasting shapes of fruits, ranging from elongated, that are much longer than wide, to others that are wider than long and almost disk-shaped. The shapes of the fruits are determined by the rates of growth in various directions, and these rates are ultimately regulated by systems of genes. According to Sinnott (1922, 1927) and Sinnott and Hammond (1930), the ratio of length to width of the fruits of various cultivated races of *Cucurbita pepo* is determined by several genes, some of which are oppositional in their effects.

A series of four pairs of genes, A to D, tend to shorten the longitudinal axis of the fruit. These genes are counterbalanced by one or possibly several pairs of an I series that tend to lengthen the fruit, either directly or by inhibiting the shortening effect of the A to D genes. The genic balance is such that in heterozygous condition one I gene is able to counteract one pair of shortening genes. Likewise, the homozygous presence of II almost completely obliterates the effect of two pairs of the shortening genes, so that the fruit becomes longer than wide. Different biotypes can produce isodiametrical fruits, for example those that possess one pair of shortening genes and no I genes, and others that possess two pairs of shortening genes counterbalanced by one I gene in heterozygous condition.

Various cultivated races of *Cucurbita pepo* apparently possess different combinations of this genic balance system, even though phenotypically they may be fairly similar. Accordingly, several of the F_2's, or even backcrossing of interracial hybrids, may show extensive transgressive segregation.

Multiple genes in Lamium. *Lamium maculatum* L., $n=9$, the deadnettle of the mint family, has a rare variant in which the stem ends in a top flower that is peloric and actinomorphic, not zygomorphic as is normal in Labiates. Sirks (1925) found that a peloric form produced only pelorics by selfing, and the normal form, likewise, when selfed produced only normal progeny. A reciprocal cross between normal and peloric produced 1106 F_1 plants, all normal. Five of the F_1 plants were selfed. One of these segregated in the ratio 15 normal to 1 peloric, and when backcrossed to the peloric parent it segregated 3:1. Another F_1 plant segregated in the ratio 63:1, and in the backcross, 7:1. Two other selfed F_1 plants segregated in the ratio 255:1, and in backcrosses, 15:1. The fifth F_1 plant produced 275 normal and no pelorics, and in the backcross, 349 normal and 17 pelorics. The last was probably also a four-gene segregation. The normal parent was evidently heterozygous for at least two of the four dominant genes that determine the usual growth type of the inflorescence which prevents peloric flowers from appearing. Any one of the four multiple dominant genes of this series assures the normal kind of inflorescence. The extra multiples operate to submerge the recessive phenotype, which appears only rarely.

Plantago major. The common plantain, *Plantago major* L., of the Plantaginaceae, is a highly adaptable cosmopolitan weed that, with *Plantago lanceolata* L., has followed man from temperate to tropical latitudes. These two plantains are among the few plants that are able to tolerate climatic differences over such wide ranges of latitude. They are among man's earliest weeds. In Denmark and probably also elsewhere, their pollen suddenly appeared in deposits of late stone age formed about 4000 years ago, together with pollen of cereals and bits of charcoal that indicate that the primeval forest had been burned (Iversen, 1941, 1949). As a neolithic farming people took possession of the country, the appearance of *Plantago* was followed by a reduction in the amount of tree pollen and an increase in pollen of herbaceous plants.

These two species of *Plantago* have remained diploid, with only six pairs of chromosomes (Turesson, 1938, *P. major;* Böcher, 1943, *P. lanceolata*). Hammarlund (1921, 1927) made an extensive analysis of the genes that control two characters in *Plantago major.* He found that a system of four pairs of multiple genes having cumulative effects regulate leaf color, and that at least two pairs of genes of oppositional effect regulate development of the spicate inflorescence. At that time it was generally assumed that multiple genes were a reflection of the degree of polyploidy, but the chromosome number of *Plantago major* was not known until 11 years later.

For one of his crossings Hammarlund (1927) used as the maternal parent a teratological strain which he called "pyramidal." It had normal rosette leaves but abnormal inflorescences with small petiolate leaves instead of normal inconspicuous bracts subtending the flowers of the elongate spicate inflorescence. The leaflike bracts gave the inflorescence a pyramidal appearance. A small colony of the pyramidal strain was discovered near Vaxholm, Sweden, only a few feet removed from plants of the common type of *Plantago major.* The strain with the new kind of inflorescence, therefore, made its appearance under circumstances similar to those of *Capsella heegeri* mentioned in earlier pages. The pyramidal strain was pollinated by a strain that Hammarlund had named "rubra" on account of its deep red leaves; it had been found growing wild in the Botanical Garden at Lund, Sweden, and had the normal spicate inflorescence of *P. major.*

The F_1 hybrid harvested on the green pyramidal plant had normal spikes with inconspicuous bracts but fairly dark red leaves. Although generally considered to be wind pollinators, these strains of *Plantago* proved to be self-compatible and produced many seeds by selfing. In the F_2 a six-gene segregation was found to govern spike characters and leaf colors, and a new phenotype made its appearance, the so-called "rosette" form. In "rosette," the bracts of the inflorescence became as large as the basal rosette leaves, and the axis of the spike was much shortened in contrast with both the parental strains, which had long spikes.

The F_2 consisted of 4949 plants, and all six of the possible phenotypes were represented among the progeny. Table 60 lists the characters and the genic

formulas of the parents and of the F_1 in addition to the observed and calculated F_2 frequencies. In this 6-chromosome species, segregations for the phenotypes governed by six pairs of genes appeared to occur without indication of linkage. In leaf color the segregation was in the ratio 255 red to 1 green, indicating segregation for four multiple genes. With respect to the inflorescence, the F_2 segregated in the ratio 12 normal to 3 of rosette type to 1 pyramidal. For this character, therefore, the parental strains differed by two pairs of genes.

TABLE 60

INHERITANCE OF INFLORESCENCE TYPE AND LEAF COLOR IN PLANTAGO MAJOR. FREQUENCIES OF PHENOTYPES AND GENOTYPES IN F_2. (AFTER HAMMARLUND, 1927.)

Pyramidal, $bbccr_1r_1r_2r_2r_3r_3r_4r_4$ ——— × ——— Rubra, $BBCCR_1R_1R_2R_2R_3R_3R_4R_4$
leafy bracts, green leaves — inconspicuous bracts, deep red leaves
F_1: $BbCcR_1r_1R_2r_2R_3r_3R_4r_4$, inconspicuous bracts, red leaves

F_2 FREQUENCIES

SPIKE AND BRACTS	LEAF COLOR		TOTAL	CALCULATED	RATIO
	Red R·······	Green $r_1r_2r_3r_4$			
Normal, BC	3724	19	3743	3711.8	12
Rosette, bbC	887	2	889	927.9	3
Pyramidal, bbcc	314	3	317	309.3	1
Total	4925	24	4949	4949.0	16
Calculated	4929.7	19.3	4949.0		
Ratio	255	1	256		

bbcc: basic recessive genotype, producing long spike and fairly leafy bracts; producing phenotype "pyramidal."
C: gene shortening spike and lengthening bracts to leaf size; producing phenotype "rosette."
B: gene lengthening spike and shortening bracts to inconspicuousness, epistatic over C; producing phenotype "normal."
R_1 to R_4: dominant, multiple genes producing red color in leaves; the recessive genotype, $r_1r_1r_2r_2r_3r_3r_4r_4$, has green leaves.

It is rather unusual to encounter in an epistatic series of three phenotypes a situation such as that of the *Plantago* inflorescence in which the basic recessive is phenotypically intermediate between the most epistatic type and number 2 in the series. The pyramidal form bbcc is the basic recessive. Morphologically the pyramidal form is less specialized than the normal form, because it consists of a stem with functional leaves, the flowers being borne in the axils. The dominant gene C changes the subtending small leaves so that they equal the basal rosette leaves in size and shape. This gene also shortens the shoot, reducing the inflorescence strikingly in length, so that the bbC biotype, named "rosette," becomes a compound rosette with very few flowers in the axils of the leaves of the secondary rosettes. The addition of the epistatic B gene to the "rosette" form lengthens the axis of the spike again and shortens the bracts.

There is also a third gene, N, that controls the development of the normal inflorescence. It is dominant, and suppresses a tendency to develop branched spikes, nn. The Nn heterozygote in *Plantago* is highly modifiable, however, so that in certain years it may be normal and in others have branched inflorescences (Hammarlund, 1921).

It is highly probable that the pyramidal biotype is not actually the basic recessive in *Plantago major.* The segregation of the two or three genes here discussed, however, indicates the genetic changes that may have occurred as the type of inflorescence now found in *Plantago major* and *P. lanceolata* evolved through geologic periods.

Further support for the theory that four pairs of multiple genes govern red leaf color in *Plantago major* was obtained by Hammarlund (1927), who tested 862 F_3 progenies from red F_2 plants totaling about 990,000 F_3 individuals. Among the 862 F_3 progenies, 619 proved to contain red only in various shades; 40 segregated in the ratio 255:1; 104 in the ratio 63:1; 71 as 15:1; and 28 as 3:1. The observed frequencies of segregation in the F_3 are very close to the calculated ones. It is significant that in a geologically old but diploid species as many as four pairs of genes of approximately similar effect may regulate leaf color.

In this connection it is of interest that Ikeno (1927), who investigated the inheritance of variegated white-striate leaves in *Plantago major,* found that the variegated type was controlled by nuclear genes which segregated in the ratio 15 green to 1 variegated, another example of polymeric genes in this diploid species.

MULTIPLE GENES IN DROSOPHILA MELANOGASTER. That the 4-chromosome fruit fly *Drosophila melanogaster* may have multiple genes determining a character was shown by Wexelsen (1928) in an investigation on the number of vessels (spermothecas) that are attached to the female uterus and serve as depositories for the sperm. Normally, individuals of this *Drosophila* have two of these vessels, but a strain was developed having three spermothecas instead of two. Crossing of a three-spermotheca form with the normal yielded a normal type F_1 having two spermothecas. Backcrosses between the F_1 and the recessive three-spermotheca form produced 413 normal females to 52 recessive-type individuals, approximately a 7:1 ratio. This ratio would indicate that three multiple dominant genes suppress the development of the third spermotheca, and that the presence of a single one of the dominant genes is sufficient to prevent the third spermotheca from developing. The three genes for the normal condition were located in the second, third, and fourth chromosomes.

SYSTEMS OF GENES IN WILD PANSIES, VIOLA TRICOLOR AND V. ARVENSIS. A remarkable and complex genetic control of a minute character was shown to exist in wild forms of the *Viola tricolor-arvensis* complex of the violet family (Clausen, 1926, 1951). *V. tricolor* L. has 13 pairs of chromosomes, and *V. arvensis* Murr.

17 pairs, but the interspecific hybrid between them is sufficiently fertile to permit genic analysis.

Some forms of this species complex have a dark, cuneiform mark, the so-called honey spot, on the front of the pistil, and other forms lack this ornamentation. This inconspicuous spot is controlled by a series of at least four pairs of multiple genes. In certain forms of the two species a positive gene for pistil spot, S, requires the presence of a complementary gene, K, before it can express itself. Other forms have complementary inhibitors, I and H, that can cover the effect of the genes for spot. Nonspot, accordingly, can be either dominant or recessive, and in the next generation the recessive phenotype may segregate the apparent dominant form. This arrangement of complementary positive genes combined with complementary inhibitors can result in highly different F_2 ratios of segregations, as shown by those presented in table 61.

TABLE 61

VARIOUS KINDS OF F_2 SEGREGATION GOVERNING SPOTTED PISTILS IN VIOLA

Character	Genotypes in F_1 and ratios of F_2 segregations				
	SsKKiihh	SsKkiihh	SSKKIiHH	SSKKIiHh	SsKKIiHh
Spot	3	9	1	7	21
Nonspot	1	7	3	9	43

S: gene for style spot, inactive by itself.
K: complementary gene for style spot, activating S.
I: gene inhibiting style spot; inactive by itself, but activated by the complementary gene H.
H: complementary gene inhibiting style spot; activates the I gene but inactive by itself.
The IH combination is epistatic over SK.

The highly variable petal colors of the wild pansies are controlled by an even more impressive series of at least ten pairs of genes (Clausen, 1926, 1931, 1951). Velvety black is the most recessive phenotype in this series, and ivory white the most dominant. Only through backcrossing to velvety black was it possible to obtain populations that were large enough to determine the number of genes involved (Clausen, 1930).

Three pairs of multiple basic genes, A_1 to A_3, control the production of anthocyanin in the petals; the presence of any one of them is sufficient to ensure full coloration, whereas plants recessive for all three have pure white petals (see formulas of genotypes in table 62). A reaction gene, R, determines whether the anthocyanin is purple to black or pink to deep velvety rose, rr. If no genes other than A and R are present, the color of the petals is deep velvety black, which is found in a rare cultivated garden form of *Viola tricolor* dating back to the time before this species had been intercrossed with the 24-chromosome *Viola lutea* Huds., whereby the modern pansies were produced.

A series of dominant epistatic modifier genes, M_5 to M_1, modify in distinct steps velvety black to the violet or purple of the common wild *Viola tricolor*.

The modifier genes form a successively epistatic series with M_1 as the top epistatic gene which produces the violet color of wild *Viola tricolor* irrespective of the presence or absence of any of the others of the series. Velvety 1, $m_1m_1M_2$, is the first step toward black, and causes the two petals to be dark velvety; velvety 2, $m_1m_1m_2m_2M_3$, has, in addition, a triangular velvety spot on the spur-bearing petal, whereas velvety 3, $m_1m_1m_2m_2m_3m_3M_4$, has a deep velvety border along the tips of the three lower petals in addition to the completely velvety upper two petals. In velvety 4, $m_1m_1m_2m_2m_3m_3m_4m_4M_5$, all petals are black

TABLE 62

GENES CONTROLLING PETAL COLOR IN THE SPECIES COMPLEX VIOLA TRICOLOR

Genes	Color
$A\cdots\cdots WWYYR\cdot M_1\cdots\cdots\cdots$	ivory = *V. arvensis* and *V. kitaibeliana*
$A\cdots\cdots wwYYR\cdot M_1\cdots\cdots\cdots$	yellow = *V. lutea* and *V. tricolor alpestris*
$A\cdots\cdots wwyyrrM_1\cdots\cdots\cdots$	rose pink; form of *V. tricolor*
$A\cdots\cdots wwyyR\cdot M_1\cdots\cdots\cdots$	violet = *V. tricolor*
$A\cdots\cdots wwyyR\cdot m_1m_1M_2\cdots\cdots\cdot$	velvety 1
$A\cdots\cdots wwyyR\cdot m_1m_1m_2m_2M_3\cdots\cdots$	velvety 2
$A\cdots\cdots wwyyR\cdot m_1m_1m_2m_2m_3m_3M_4\cdots$	velvety 3
$A\cdots\cdots wwyyR\cdot m_1m_1m_2m_2m_3m_3m_4m_4M_5$	velvety 4
$A\cdots\cdots wwyyR\cdot m_1m_1m_2m_2m_3m_3m_4m_4m_5m_5$	velvety 5 = velvety black in old garden form
$a_1a_1a_2a_2a_3a_3\cdots\cdots\cdots\cdots\cdots\cdots$	albino

A_1 to A_3: multiple basic genes governing anthocyanin coloration in flowers and stems; the presence of any one is sufficient to produce full color.

R: reaction gene controlling the kind of anthocyanin coloration produced by A; if R, the shades are violet purple; if rr, they are rose pink. The basic color, if determined by AR, is deep velvety black; by Arr, it is deep velvety rose.

M_1 to M_5: a series of dominant, epistatic modifier genes that in steps modify velvety black to violet; in the presence of the top epistatic gene, M_1, the velvety black color is changed to violet; M_2 to M_5 without M_1 limit violet to certain parts of the petals only.

Y: yellowing gene epistatic over violet, M_1, but not over the more intensively velvety hypostatic colors, velvety 1 to 5.

W: whitening gene; with M_1 and Y, this gene suppresses violet coloration in the petals completely, and the petals become ivory, as in *V. arvensis.* This is dominant white, which covers the deepest coloration; it contrasts with recessive white, aa, which is albino because it lacks the basic gene for color, although all the other genes may be present.

except for a narrow light-colored zone in the center of the flower. Finally, velvety 5, $m_1m_1m_2m_2m_3m_3m_4m_4m_5m_5$, which is recessive for all five modifiers, is jet black.

A yellowing gene, Y, which controls the development of yellow chromatophores in the petals will, in the presence of the violet gene M_1 in single dose, cause the lower petals to become whitish and the upper petals to be slightly mauve; with a double dose, YY, the lower petals become deep yellow and the upper white. The reason for the apparently stronger effect of the Y gene in the lower petals is that the anthocyanin coloration is weaker in the lower than in the upper petals. The effect of the chromatophore-producing Y gene is there-

fore apparently balanced against the anthocyanin genes that induce sap coloration.

An epistatic whitening gene, W, in the presence of YY will change the color of the petals to ivory irrespective of the underlying violet color. Ivory is the color common to *Viola arvensis* and *V. kitaibeliana* Roem. et Schult., and is found also in certain forms of *V. tricolor alpestris* DC. from the Swiss Alps, which may be either ivory, $AWYRM_1$, yellow, $AwYRM_1$, or even ivory and velvety, $AWYRm_1m_1M_2$.

The action of the Y and the W genes in the *Viola tricolor* complex is similar to the counterbalancing action of the Y_1 gene on the one hand, and the W_1 and W_2 genes on the other, in *Potentilla glandulosa,* except that in *Potentilla* the Y and W genes are both duplicated, and no anthocyanin occurs in its petals. Since strong anthocyanin coloration can occur in the stems and leaves of *Potentilla glandulosa,* it is possible that in the petals the anthocyanins are inhibited by strong suppressors.

The system of genes governing petal coloration in *Viola* is intricately balanced by genes of opposite effects. Moreover, the expression of some of them appears to be influenced by temperature. In forms of $WWYYRRm_1m_1M_2M_2$, the color is velvety 1 on a background of ivory during the cool spring and fall, but becomes pure ivory without a trace of velvety purple during the warm summer. The change in color is probably due to a higher rate of production of anthocyanin during cool than during hot weather. It is in line with the fact that in *Potentilla glandulosa* the A_4 gene for anthocyanin can express itself in the cool climate at Timberline but not in the warmer climate at Stanford and Mather (pp. 80–83). The theory of Emerson (1921) that cool weather interferes with nitrogen synthesis in maize so that sugars are released for anthocyanin production also fits in with this hypothesis.

Gene systems in Layia. The species *Layia platyglossa* (F. et M.) Gray, the tidytip, exists in a great number of populations in the Coast Ranges and valleys of central to southern California (Clausen, Keck, and Hiesey, 1947*a*; Clausen, 1951). This species of the subtribe Madiinae of the Compositae has 7 pairs of chromosomes and is an obligate cross pollinator, so that its genetic analysis is more difficult than that of *Potentilla glandulosa* or the *Viola tricolor* complex, the hybrids of which can be genetically analyzed through self-pollination. Data from many crossings between plants of *Layia* representing populations having contrasting characters indicate, however, that the genetic organization controlling these characters is also complex (Clausen, 1951). Some of the observed ratios of segregation of four characters and the genes controlling them are listed in table 63.

In contrast with inland forms, maritime races of *Layia platyglossa* lack a central leader, have horizontal branches, and are late-flowering. It will be noted from table 63 that there are shifts in dominance for central leader, direction of branching, and floccoseness of the pappus. These shifts occur when genes of

TABLE 63

SEGREGATION RATIOS AND GENOTYPES OF FOUR CHARACTERS OF LAYIA PLATYGLOSSA IN F_2 PROGENIES OF CROSSINGS BETWEEN PLANTS OF WIDELY SEPARATED POPULATIONS. THE F_2'S WERE OBTAINED THROUGH MUTUAL POLLINATION OF F_1 PLANTS.

Characters, and F_2 ratios	Genotypes of parental F_1 individuals	Gene functions
Central stem Present : absent		S: dominant gene controlling presence of central stem
3 : 1	SsininK or SsInkk	ss: central stem absent
7 : 9	SSIninKk	In and K: complementary genes inhibiting S
Direction of branching Ascending-erect : horizontal		Er: basic hypostatic genetic background for erect branching H and C: complementary genes, epistatic over Er, making the branching horizontal
7 : 9	$a_1a_1a_2a_2$HhCcErEr	
13 : 3	$A_1a_1a_2a_2$HhCCErEr	
15 : 1	$A_1a_1A_2a_2$HHCCErEr	A_1 and A_2: multiple, dominant genes, epistatic over HC, making the branching ascending to erect again
Earliness of flowering Early : late		Ef: basic hypostatic genetic background for early flowering
15 : 1	$E_1e_1E_2e_2e_3e_3$LLEfEf	L: dominant gene causing late flowering, epistatic over Ef
13 : 3	$E_1e_1e_2e_2e_3e_3$LlEfEf	
63 : 1	$E_1e_1E_2e_2E_3e_3$LLEfEf	E_1, E_2, E_3: multiple, dominant genes causing early flowering; epistatic over L
Floccose hairs on pappus Floccose : trace : nonfloccose		B: basic hypostatic genetic background for bristly pappus
13 : 2 : 1	$I_1i_1I_2i_2i_3i_3$FFBB	F: dominant gene causing floccose pappus
24 : 7 : 1	$I_1i_1I_2i_2I_3i_3$FFBB × $I_1i_1I_2i_2i_3i_3$FFBB	I_1, I_2, I_3: multiple genes of additive effect reducing floccoseness, I_1 being the strongest of the three; these genes occur north of the San Bernardino Mountains
3 : 0 : 13	Ii······FfBB	I: nonmultiple dominant gene that singly can inhibit pubescence on pappus; this gene occurs south of the San Bernardino Mountains

opposite effect are balanced against each other in various ways. The ratio 13:3, which is found in the inheritance of three characters, is an indication of the presence of oppositional genes. For example, the ratio 13 ascending-erect to 3 horizontal branching suggests that the double recessive, aahh, is erect, that the addition of one gene, H, causes the branches to be horizontal, and that the addition of a second gene, A, epistatic over H, induces them to become ascending-erect again.

Floccose pappus is found only in forms from southern California south of the San Bernardino Mountains, but the genetic data indicate that the gene governing this character also occurs farther north, where it is suppressed by a multiple series of two or three pairs of relatively weak inhibitors. Forms from southern California carry a strong inhibitor which in single dose removes the floccose pubescence completely.

The inheritance of color of the ray florets in *Layia* is somewhat similar to the inheritance of white and yellow petals in *Potentilla glandulosa.* The inner Coast Range and foothill species *Layia pentachaeta* Gray, having 8 pairs of chromosomes, exists in two distinct color forms, a white-rayed form, *albida,* in the inner Coast Range, and the type form of the species, which is chrome yellow, nonbleaching, and occurs in the foothills of the Sierra Nevada. The F_1 hybrid between the two is light yellow, but the rays bleach with age so that the hybrid in mid-flower resembles a chimera with darker- and lighter-colored heads. In F_2 progeny the segregation ranges from lemon chrome through lemon yellow, martius yellow, and sea-foam yellow to the ivory of the white-rayed parent. Some of the plants having yellow colors bleach with age; others do not. In this segregation about four steps in intensity of yellow can be recognized. The yellow shades are overlayered by at least one pair of whitening genes, and by a pair of genes that induce bleaching as the flower ages.

A SYSTEM OF OPPOSITIONAL GENES GOVERNING TIME OF FLOWERING IN MADIA. *Madia elegans* Don., the common Madia, is an 8-chromosome annual species in California belonging to the Madiinae. In the Coast Ranges and foothills it has evolved both a spring- and a fall-flowering race (Clausen, 1951). Both germinate in fall and winter; the spring race flowers early in the season from March to May without developing rosette leaves, and withers after its seeds have ripened. The fall race develops only a dense basal rosette of leaves and a long taproot during the entire spring, and does not begin to develop flowering stems until midsummer. When it finally reaches this stage, it produces giant stems densely covered with highly glandular leaves, in marked contrast with the short-stemmed spring race, which has only small, scattered, almost nonglandular leaves. The most extreme late-blooming forms do not begin to flower in the garden at Stanford until after August 1, two months after the spring race has dried completely. The late form has been called var. *densifolia* (Greene) Jeps.

By forcing growth of the fall-flowering race of *Madia elegans* in a greenhouse and keeping the spring-flowering form out-of-doors, it was possible to cross the

two (Clausen, 1951). The hybrid was found to be fairly early, and flowered approximately 2 weeks later than the spring-blooming parent. In a large F_2 consisting of more than 1100 plants, nearly three-fourths of the progeny flowered in May together with the spring-blooming parental race, as shown in table 64. Only about 1 among 64 flowered within the range July 9 to August 1, the span of the fall-flowering race.

Apparently the spring form possesses one pair of dominant and epistatic genes for earliness, EE, whereas the fall-blooming race is recessive for the E genes and possesses at least two pairs of multiple genes, L_1 and L_2, for lateness, having the formula $eeL_1L_1L_2L_2$. The early flowering of the F_1, and the observed ratios in the F_2, suggest that the effect of the L genes is largely counterbalanced by the presence of either one of the two E genes.

TABLE 64

INHERITANCE OF EARLINESS OF FLOWERING IN MADIA ELEGANS

Spring-blooming race, *vernalis* ———— × ———— fall-blooming race, *densifolia*
May, $EEl_1l_1l_2l_2$ — August, $eeL_1L_1L_2L_2$

F_1: June 1, $EeL_1l_1L_2l_2$

F_2 FREQUENCIES

Date of first flowers	Genotypes	Observed	Calculated	Ratio
May 10 to 31	$E\cdots\cdots$	796	851.2	48
June 1 to July 8	$eeL_1\cdots$ to $eeL_1L_1L_2l_2$	323	266.0	15
July 9 to August 1	$eeL_1L_1L_2L_2$	16	17.8	1
Total		1135	1135.0	64

E: dominant and epistatic gene causing early flowering.
L_1 to L_2: multiple cumulative genes causing late flowering; hypostatic under E.

The existence of even earlier races than the spring form used indicates that the species may have more than one pair of genes for earliness. The fact that scarcely any plants as late-blooming as the fall-blooming parent were obtained in the F_2 likewise suggests that more than two pairs of genes for lateness are operating. The F_2 population of 1135 individuals was scarcely large enough to reveal the number of genes in a system of this kind, but the data are reasonably indicative of the existence of at least one pair of genes regulating earliness which is epistatic and to some extent balanced against at least two pairs of genes delaying flowering.

GENE SYSTEMS REGULATING BIOCHEMICAL AND PHYSIOLOGICAL EFFECTS AND THEIR EXPRESSION IN DIFFERENT ENVIRONMENTS

Genes appear to govern the production of chemical substances that control growth and other physiological processes in organisms, which, in turn, are

influenced by environment. Although our current understanding of the intermediate steps is still incomplete, data throwing light on them are steadily increasing. A few notable examples will be reviewed, since they suggest the manner in which the phenotypic expression of gene systems of ecological races may be modified when the races are grown in different environments, as outlined in chapter III.

The colors of animals and plants were among the first genetically controlled characters to be associated with differences in biochemical composition. In 1915 Onslow reported that chloroform extracts of skins of black-, blue-, and chocolate-colored rabbits contained the enzyme tyrosinase, which was lacking in extracts of skins of recessive white and yellow rabbits. Wright (1916, pp. 68–112, 118) and Goldschmidt (1916; 1938, p. 91) early emphasized the importance of the relations between the genes, the enzymes, and their phenotypic expression.

In plants the biochemical relations of gene-controlled colors of flowers were considered by Wheldale (1911, 1914) and Wheldale-Onslow (1925, 1931, 1932). Scott-Moncrieff (1936) and Lawrence and Price (1940) reported relatively simple gene-controlled biochemical differences between petal colors of various strains of *Petunia* and *Dahlia*.

An important step in integrating genetics and biochemistry was made by Beadle and Tatum in their investigations on the bread mold, *Neurospora crassa* (Beadle, 1949). Information on the genetic control of the manufacture of specific amino acids in normal *Neurospora* was obtained indirectly by producing the recessive mutations of the genes controlling the synthesis of specific amino acids. The mutants were recognized by their failure to synthesize one of the amino acids that is essential for the growth of the mold; the mutated strain died unless this acid was added to the medium on which it was cultured.

In man, several recessive genes cause seemingly unrelated diseases, but physiologically and biochemically these have been found to be connected with failures at different points in the breakdown of a single nutritionally essential amino acid, phenylalanine (Beadle, 1949; Srb and Owen, 1952). Persons suffering from phenylketonuria, a form of juvenile feeblemindedness, fail to oxidize phenylpyruvic acid, one of the derivatives of phenylalanine, and others suffering from alkaptonuria, the black urine disease, are recessive for another pair of genes that are essential for the oxidation of homogentisic acid, a different step in the breakdown of phenylalanine. Another recessive defect in man, albinism, appears to be related to failures in the breakdown of two amino acids, for melanin, occurring in the skin of nonalbino persons, is a derivative both of phenylalanine and of tyrosine.

Three examples of the integration of gene action with physiological and biochemical processes will be discussed in the following pages.

THE PHYSIOLOGICAL ACTION OF WAXY VERSUS STARCHY GENE IN MAIZE. One of the simpler relations between a gene and its physiological expression appears to exist in the Wx versus wx genes for starchy as contrasted with waxy endosperm

and pollen grains in maize. G. N. Collins (1909) called attention to the existence of the waxy character in the endosperm of a strain of maize from China, and Collins and Kempton (1913) showed that waxy is a simple recessive to starchy. Weatherwax (1922) pointed out that the carbohydrate in waxy endosperm differed from that in starchy endosperm. Demerec (1924) and Brink and MacGillivray (1924) simultaneously reported that the difference in carbohydrate also appeared in the pollen, and that pollen grains of two kinds were found in the heterozygotic F_1 hybrids. Starchy grains stained purple when treated with iodine, whereas waxy grains became reddish. A gametic segregation ratio of 1 : 1 could thus be directly observed on the pollen.

Brink and Abegg (1926) found that both waxy and nonwaxy pollen contained starch and dextrin, and that the proportion of the two components was approximately the same in the two kinds of pollen. However, waxy had proportionately more sucrose than was found in starchy, and starchy had more of the reducing sugars. Brink and Abegg also found that both kinds of pollen contained the starch amylose in both the α and β isomeric forms. In starchy pollen, however, 92 per cent of the amylose was of the α form, whereas in waxy pollen approximately 60 per cent of the amylose was of the β form and only 40 per cent of the α form.

In exploring the kinds of enzymes that hydrolyze carbohydrates in waxy and nonwaxy plants, Brink (1929*a,* 1929*b*) found that both yielded only maltose when exposed to the action of malt diastase. Both kinds of pollen were also found to contain amylase. Crude extracts from the two kinds of pollen, each containing its characteristic blend of amylases, differed, however, in the speed of their hydrolyzing effects. Starch pastes from waxy pollen consistently reacted more slowly than those from nonwaxy, irrespective of whether the hydrolyzing effect was tested on potato starch, waxy maize, or nonwaxy maize. The single-gene difference between the two kinds of maize expresses itself, therefore, in a significantly higher diastatic activity in the nonwaxy than in the waxy biotype. Similar differences might be expected to exist among the biochemical systems that are set in motion by biotypes having sugary versus starchy endosperm in maize, and sugary versus starchy embryos in the seeds of peas, both of which are one-gene differences.

Multiple genes in yeasts controlling the production of enzymes. Winge and Roberts have shown that in members of the yeast family the fermentation of specific sugars can be controlled by series of multiple genes. In yeasts there is an even more immediate connection between the gene and the character it controls than between the waxy gene and its expression in the pollen of maize. The various species of yeast produce specific kinds of enzymes, and the presence of the enzyme is recognized by its fermenting effect on specific sugars. The substratum on which the yeast enzyme works is outside the organism, and can be supplied in the form of accurately controlled media, whereas in more complex organisms the substrate is manufactured within the organism itself and

is therefore beyond direct experimental control. The yeasts accordingly provide a convenient means for studying the relations among genes, enzymes, and biochemical processes.

Some of the yeasts used in these investigations date back to the classic investigations of Emil Christian Hansen. They exhibit distinct haplo- and diplophases (Winge, 1935; Winge and Laustsen, 1937), although their pattern in this respect is not so rigidly set as in higher plants (Winge and Roberts, 1954*a,* 1954*b*). This flexibility in the hereditary mechanism of the yeasts sometimes affects the genetic ratios. To explain the deviating ratios, other yeast geneticists have proposed auxiliary hypotheses postulating cytogenes and gene conversion (Lindegren, 1949, 1953). Winge and Roberts (1952), however, used a refined technique of isolating individual genes of a multiple series from other genes in the series, and incorporating the individual genes into separate strains.

Techniques were developed during the early stages of the yeast investigations that made it possible to cross distinct races, species, and even genera, and to germinate individually the four spores of the ascus (Winge and Laustsen, 1939; Winge, 1942, 1949). Interspecific hybrids of yeasts resemble interspecific hybrids of higher plants in that some are highly sterile, grow slowly, and segregate weak offspring (Winge and Laustsen, 1938, cf. plates V, VI of Danish baking yeast × *Saccharomyces validus*). Crossings frequently fail completely, as, for example, between *S. chevalieri* and *S. mangini,* or *S. dairensis* and *S. unisporus* (Gilliland, 1949). If F_1 hybrids are formed, the spores may fail to germinate, as in *S. validus* × *S. italicus*: sometimes the germination percentage is very low, as when *S. validus* or *S. italicus* is crossed with a Danish baking yeast type, or with *S. cerevisiae* (cf. Winge and Laustsen, 1939, table on p. 346). The species *Saccharomyces cerevisiae, S. italicus,* and *S. chevalieri,* however, are physiologically and genetically closely enough related so that germination percentages of hybrid spores are sufficiently high to permit reliable genetic work. Winge and Roberts used only data from asci in which all the four spores were able to germinate and develop.

The chromosomes of yeast are so small that they cannot be counted successfully, but the nucleus can be recognized, and the stages in germination of the spores, conjugation, and development of the diploid phase can be studied (Winge, 1935; Winge and Laustsen, 1937). The diploid fertilized cells are more elongate than those of the haploid phase. Curiously enough, the common denominator in the interspecific crossings, *Saccharomyces chevalieri,* is a homothallic species so that self-fertilization can occur, and it also has a gene D which is responsible for obligatory diploidization of single-spore cultures (Winge and Roberts, 1949). In crossings between *S. chevalieri* and a species that does not have this character, the asci of the F_1 hybrid segregate, so that two spores diploidize, preventing later mating, and two produce haploid cultures. This accommodating characteristic made it possible to produce homozygous strains directly from spores. Strains used by American investigators do not have this gene and remain haploid until crossed (Winge and Roberts, 1955).

The technique for isolating each gene of a multiple series in separate strains made it possible to overcome certain innate difficulties in the yeast organism and to discover the processes that each gene controls. A remarkable sequence of relationships has gradually been unfolded in a series of papers identifying the genes that control various fermenting processes of three of the species of yeast (Winge and Roberts, 1948, 1949, 1950, 1952, 1953, 1954*a*, 1954*b*, 1955; Winge, 1949, 1952; Gilliland, 1949; Jinks, 1953). A condensed summary of the effects of each gene in the gene systems of the three species will be presented below.

1. *Saccharomyces cerevisiae* Hansen, strain "Yeast Foam": genotypic formula, $M_1M_1M_2M_2M_3M_3r_1r_1R_2R_2r_3r_3GG$. *Saccharomyces cerevisiae* is a baking yeast that also is used as a top yeast in brewing beer of low alcoholic percentage. "Yeast Foam" is an old American commercial strain of slowly acting baking yeast. Three pairs of multiple M genes govern the fermentation of the disaccharide maltose (Winge and Roberts, 1948, 1950). The R_2 gene, on the other hand, controls the fermentation of the trisaccharide raffinose, and of the disaccharide sucrose (Winge and Roberts, 1952, 1953). The G gene, finally, controls fermentation of the monosaccharide galactose (Winge and Roberts, 1948). The Yeast Foam strain is therefore capable of breaking down a number of carbohydrates.

It was found in detailed investigations that the M_1 gene is responsible for the synthesis of the enzyme α-glucosidase, which, in turn, promotes rapid fermentation of maltose (within a few hours), and slow fermentation of sucrose (after an interval of several days). The M_2 and M_3 genes, on the other hand, are independently responsible for the synthesis of the enzyme maltase, which rapidly ferments maltose but not sucrose. The M_1 and M_2 genes of this multiple series differ, therefore, in their chemical action. The M_2 and M_3 genes are so similar in their action that it has been impossible to distinguish between them except through isolation and genetic testing against each other. The two genes tested are identical if the hybrid does not segregate, but distinct if the hybrid produces a two-gene segregation (Winge and Roberts, 1952). There is no cumulative effect when more than one of the dominant M genes are present. The function of the duplication in the M genes therefore seems to be to ensure multiple control of a vital process. The recessive alleles, m_1 to m_3, are apparently without any influence on the fermentation of maltose. No fermentation occurs in a maltose culture of a triple recessive strain even after long periods, whereas the presence of just one of the dominant M's is sufficient to promote rapid maltose fermentation.

It was found by X-raying (Winge and Roberts, 1950) that M_3 could mutate to m_3. A spontaneous mutation from m_1 to M_1 was discovered as well, indicating that mutations can also take place from the recessive to the dominant state. In following this lead, a triple recessive strain $m_1m_1m_2m_2m_3m_3$ was irradiated, and a mutation to a dominant and rapidly maltose-fermenting M type was found. The new mutant, however, yielded two-gene segregations when crossed to any one of the dominant M_1, M_2, or M_3 types, indicating

that it was not identical with any of them, and was therefore apparently a dominant mutation from a fourth gene in the series, m_4, mutated to M_4. Later a nonirradiated culture which was triple recessive for the m_1 to m_3 genes produced spontaneously a dominant maltose-fermenting biotype. In systematic hybridizations with the M_1, M_2, and M_3 test cultures, all trials of the spontaneous mutation yielded two-gene segregations, whereas a hybrid between it and M_4 produced by irradiation yielded maltose-fermenting progeny and did not segregate. Accordingly, the spontaneous and the irradiated mutants were identical, and both had arisen through dominant mutation of a hitherto unnoticed recessive locus (Winge and Roberts, 1950). The M_4 gene has the same effect as M_2 and M_3, but apparently it is located in a different chromosome from any of the other three of the series.

Besides the M series, the Yeast Foam strain of *S. cerevisiae* contains also one dominant gene, R_2, of a series of three pairs of multiple genes governing the fermentation of raffinose. *Saccharomyces chevalieri* possesses the three raffinose genes, R_1 to R_3, all in the dominant condition. Like the other two genes of its series, the R_2 gene is responsible for the synthesis of the enzyme β-h-fructosidase, which is a rapid fermenter both of raffinose and of sucrose. The latter action is in contrast with that of M_1, which ferments sucrose slowly.

Finally, *Saccharomyces cerevisiae* has a dominant gene, G, which is capable of rapidly producing galactozymase and of fermenting galactose (Winge and Roberts, 1948; Winge, 1952). Galactose is a monosaccharide formed through, first, the breaking down of raffinose to fructose and the disaccharide melebiose, and next hydrolyzing melebiose down to glucose and galactose. No multiples of the G gene have been found by Winge in any of the yeast species. Lindegren (1949) appears to have possessed such a multiple.

A weak galactose-fermenting gene, g^s, exists, however, in *Saccharomyces chevalieri*. The g^s gene is able to promote fermentation of galactose, but only after the yeast has been exposed to a galactose substrate for 4 to 6 days or longer. After such a period, the galactose fermentation by the g^s biotype is as rapid as in the dominant G biotype, and the yeast will continue to ferment rapidly. If the old substrate in which the g^s yeast has been kept is completely removed, then another adaptive period of 4 to 6 days is required before the g^s biotype will ferment galactose. Winge and Roberts (1948) and Winge (1952) suggest that the reason for this delay in action is that the rate of enzyme production is so slow in the g^s strain that several days are required to produce sufficient galactozymase for rapid fermentation of galactose. Removal of the enzyme "de-adapts" the yeast. It is not known with certainty whether g^s is an allele of G, or whether it is a weaker G gene, G_2, in a different chromosome and hypostatic under the G gene, G_1. If all species were homozygous for G_2, and G_1 were epistatic over G_2, the same genetic effect would be produced as if G and g^s were alternate genes at the same locus.

2. *Saccharomyces chevalieri,* genotypic formula

$$m_1m_1m_2m_2m_3m_3R_1R_1R_2R_2R_3R_3g^sg^s.$$

Saccharomyces chevalieri is a homothallic species that is recessive for all m genes, and therefore unable to ferment maltose (Winge and Roberts, 1950). It has, however, a multiple series of three pairs of genes, R_1 to R_3, which enable it to ferment raffinose and sucrose (Gilliland, 1949; Winge and Roberts, 1952; Winge, 1949, as an S series), and it also has the g^s gene for slow fermentation of galactose. Gilliland's analysis was performed through a cross of *S. chevalieri* with *S. italicus,* which, unlike *S. cerevisiae,* is recessive for all R genes. The data were insufficient to prove the existence of three multiples, but Winge and Roberts (1952) isolated the three genes into separate strains and proved that they were at different loci, and apparently in different chromosomes. Each R gene synthesizes the enzyme β-h-fructosidase, which, in turn, ferments raffinose into fructose and melebiose, and sucrose into glucose and fructose. No differences were discovered among the three R genes, and each of them is able to operate independently of the others. The action of the g^s gene was discussed under *S. cerevisiae.*

3. *Saccharomyces italicus* Castelli, genetic formula

$$M_1M_1m_2m_2m_3m_3r_1r_1r_2r_2r_3r_3GG.$$

Saccharomyces italicus is a wine yeast. Its possession of the M_1 gene enables it to ferment maltose rapidly, and sucrose slowly. Being recessive for all r genes, it is unable to ferment raffinose. It has, however, the G genes for the rapid fermentation of galactose.

It was discovered in crossings between *S. italicus* and *S. chevalieri* that the M_1 and r_1 genes of *italicus* and the m_1 and R_1 genes of *chevalieri* are closely linked. In the F_2 progeny the ability to ferment maltose rapidly and sucrose slowly is linked with the inability to ferment raffinose. On the other hand, ability to ferment both raffinose and sucrose rapidly was always combined with the inability to ferment maltose. It was not known whether or not the two were at separate loci until rare crossover types were obtained of M_1R_1 that were able to ferment both maltose and raffinose, and also forms of m_1r_1 that were unable to ferment either (Winge and Roberts, 1952). By crossing the two crossover types, M_1R_1 and m_1r_1, the R and the M genes again exchanged locations through a second crossing-over, and the original combinations M_1r_1 and m_1R_1 were obtained. The frequency of crossover is of the order of about 1 per cent.

COMPLEMENTARY GENES GOVERNING CYANOGENESIS IN LEGUMES. Certain forms of white clover, *Trifolium repens* L., $n=16$, are able to release hydrogen cyanide from the leaves and stems when injured or killed. This effect depends upon the presence of a gene, Ac, for production of the glucoside lotaustralin, $C_6H_{11}O_5 \cdot O \cdot C(CH_3)(C_2H_5) \cdot CN$, named after *Lotus australis,* from which it was first isolated. This cyanogenetic glucoside is very similar to another, linamarin, $C_6H_{11}O_5O \cdot C(CH_3)_2 \cdot CN$, also found in white clover but originally isolated from flax, *Linum.* The liberation of hydrogen cyanide depends upon the presence of the enzyme linamarase, which hydrolyzes the glucosides into

their components. Linamarase, in addition to occurring in flax seeds, is also found in white clover, where its presence is controlled by the dominant gene Li. The liberation of hydrogen cyanide depends upon the complementary action of the Ac and Li genes.

Some clovers have one of these, others the other, and many have both. Papers by Williams (1939), Dawson (1941), Atwood and Sullivan (1943), and Daday (1954) have clarified the nature of the cyanogenetic reaction. Briefly, the loss of transport animals by poisoning during the Sudanese campaign of 1896–1900 led to the isolation of the cyanogenetic constituent from *Lotus*. Later the glucosides were isolated biochemically from white clover in New Zealand.

By crossing cyanogenetic white clover with noncyanogenetic strains, Williams obtained an F_2 segregation of 1219 cyanogenetic to 424 noncyanogenetic individuals, and a backcross proportion of 1922:1887. He was therefore able to demonstrate that the difference depended upon the action of the single dominant gene. Corkill (1940) developed separate tests for determining the presence of the glucosides and of the enzyme which Atwood and Sullivan utilized in classifying F_2 plants of the backcrosses. Finally, Daday (1954) used these tests for a determination of the presence both of the glucoside and of the enzyme in populations of *Trifolium repens* from western, central, and southern Europe, Asia Minor, and Lebanon-Palestine; he found that the presence of both decreases sharply in areas where the January mean temperature is below the freezing point. Indirectly these tests indicate also the presence of the Ac and the Li genes.

The relatively simple two-gene ratio found to govern the presence of the glucoside and the enzyme does not exclude the possibility that genetic control may actually be more complex. Williams' extensive experiments give the impression of even simpler control, because in his crosses apparently both parents were of such a constitution as to yield simple 3:1 ratios. In *Lotus corniculatus* L., Dawson (1941) also found a difference in only one of the two controlling genes; the enzyme was apparently present in all cultures that segregated for the glucoside reaction. *Lotus* is tetraploid, however, and behaves as an autotetraploid. The gene governing glucoside production is therefore duplicated, so that tetrasomic ratios of 5:1, 11:1, and 35:1 were observed in addition to the ordinary monogenic 1:1 and 3:1 ratios, although apparently the chromosomes associated in pairs. Dawson found that none of 13 populations of *Lotus uliginosus* Schrank. contained the glucoside, that only 4 of 401 individuals of 8 populations of *L. tenuis* W. et K. had the glucoside, but that all of 20 population samples of *L. corniculatus* contained some plants with and others without the glucoside.

Phenotypic expression of genotypes over a range of environments. Few investigations have been made on the responses of different kinds of organism in a range of environments. There are enough examples, however, to indicate

that the principles developed in the study of *Potentilla glandulosa* have general validity among various kinds of living things.

Modification in a genetically controlled petal color was reported by Baur (1914, p. 8) in *Primula sinensis rubra.* At low temperatures of 15° to 20° C. it had red petals, but changed to white at temperatures above 30° to 35° C. This kind of change is opposite in direction to that found in the *Potentilla* biotypes, which became whiter at the cool Timberline station, but it is in accord with the modification in *Viola arvensis velutina,* $WWYYm_1m_1M_2M_2$ (p. 190), which had deep velvety purple upper petals in spring and fall, but became ivory during the hot summer months (Clausen, 1926, p. 51; 1931).

A somewhat similar situation was found in the so-called Himalaya rabbit. Goldschmidt (1938) called attention to an early experiment by Schultz (1915–1916, 1928) indicating that the white Himalaya rabbit, which has black feet, and black tips on the nose, ears, and tail, may, under cool conditions, develop black color in the body coat also. If the black hairs on the body are shaved off and the animal is kept under warm conditions, the new hairs are white. Since the extremities are the coolest parts of the body, the dark color develops there first. The extension of the dark color to other parts of the body depends upon the temperature to which the animal has been exposed, and upon gene dosage, whether the animal is homozygous or heterozygous for the Himalaya gene.

A more thorough analysis of genotypes in relation to a range of temperatures was reported by Harnly and Harnly (1936) on the phenotypic expression of a series of allelic genes in *Drosophila melanogaster,* all of the vestigial group controlling wing size. The phenotypic expression was related to the temperature at which the larvae developed during a certain sensitive period. In the wild type of *Drosophila* the wing area decreased steadily as the temperature for rearing the larvae increased from 16° to 32° C.

The vestigial strain, vgvg, has rudimentary wings, and Harnly and Harnly found that, unlike the wild type, the vestigial flies reared at temperatures ranging between 16° and 29° C. developed wings that were little affected by the temperature. At 29°, however, the wing area of vestigial flies began to increase, until at 32° C. their wings approached in size those of the homozygous wild type.

In the pennant strain homozygous for an alternate of the vg gene, vg^Pvg^P, the curve for wing area decreased with temperature increase, as in the wild type, except that the larvae of homozygous pennant die at 30° C. In the heterozygote between pennant and vestigial, vg^Pvg, however, the wings likewise decrease in the temperature range from 16° to 24°, but above 24° their areas begin to increase, until at 30° C. they surpass the wild type in area. Accordingly, in the three biotypes of vestigial, pennant, and their heterozygote, the phenotypic expression of the genes follows curves that are related to temperature, but the curves are not parallel, and they may change abruptly to a different direction at certain temperatures. In flies of the vestigial series, therefore, the degree and

direction of dominance of the genes change with the temperature at which the flies have been reared.

Other examples of the interaction among genes, biochemical processes, and the metabolism of the organism have been presented in discussions by Goldschmidt (1938, 1955), Haldane (1942), Srb and Owen (1952), and Wagner and Mitchell (1955).

VARIATION EXPRESSED BEYOND THE NATURAL ENVIRONMENTAL RANGE OF THE ORGANISM. The genotype of an organism is adjusted to the environmental region in which it is native. When an organism is placed in a highly different environment, genes may come to expression for which natural selection could not have taken place in the native environment. Rather spectacular phenotypic changes may occur in this way.

Goldschmidt (1935*a,* 1935*b,* 1937, 1938) exposed larvae of *Drosophila melanogaster* to temperatures of 35° to 37° C., considerably above those at which this species normally develops. Many flies hatching from the heat-treated larvae were found to be modified. Frequently, individuals appeared that phenotypically resembled mutations which were known to occur at lower temperatures, but which were not in the ancestry of the strains used. Such modifications were termed phenocopies.

No one had previously tested *Drosophila* at these extreme temperatures. In the light of what is now known about the phenotypic expression of systems of genes, it seems highly probable that Goldschmidt's observations relate either to an activation of genes that do not come to expression within the normal temperature range for the species or to a greater "penetrance" of certain gene combinations containing oppositional genes that within the normal temperature range cancel each other.

When plants are transplanted to environments unusual for a particular strain, characters may come to expression that are not known in the native habitat of the species. Two examples will be cited here.

The tufted hairgrass, *Deschampsia caespitosa* (L.) Beauv., a 13-chromosome species, was grown at Stanford at 38° N. from seeds collected in native populations in southern Sweden at 55° N. and in southern Finland at 60° N. (Lawrence, 1945). At the southern latitude in California, about 50 per cent of the plants became viviparous in the inflorescences, a character not expressed in their native habitats in Sweden. Another species, *Deschampsia alpina* (L.) R. et S., is always viviparous in northern Europe, and taxonomists use the viviparous character to distinguish the two species, although they also differ in number of chromosomes. Apparently some individuals of *D. caespitosa* have genes regulating the occurrence of viviparism that do not come to phenotypic expression in their native environment, but do so in the experimental gardens at Stanford and Mather.

In another experiment, seedlings from several plants of a Danish coastal population of *Artemisia campestris* L. on the island of Själland, composed of

plants all having ascending-erect stems, were grown in the garden at Stanford. The 30 plants of this population grown for several years at Stanford were vigorous, but the stems were all prostrate, not ascending-erect as in the original environment.

It is obvious that gene systems of wild plants are highly dynamic in their action. For this reason the potentialities of phenotypic expression of a genotype cannot be predicted until it has been tested in a range of environments.

GENETIC SYSTEMS OF ECOLOGICAL RACES OF PLANTS

Ecological races of various families of plants adjust to differences in environment in many different ways. In the following pages some of these modes of adjustment will be discussed through examples gathered from many families of plants and from many regions of the world.

INHERITANCE IN MARITIME AND INLAND RACES OF PLANTS, SILENE. Many plant species that occupy both exposed coasts and more protected inland habitats have evolved ecologically and genetically distinct races for the two kinds of habitat (Turesson, 1922, 1925). In general, the maritime races or ecotypes are distinguished from their inland relatives by having a later period of blooming and a more prostrate growth form. One of the earliest investigations on closely related maritime and inland forms was undertaken by Marsden-Jones and Turrill (1928) on the *Silene cucubalus-maritima* complex of the Caryophyllaceae, the bladder campions of northwestern Europe.

Silene cucubalus Wibel (the Linnaean *Cucubalus Behen*) is a typical inland form which differs in many characters from its Atlantic coast relative, *Silene maritima* (Hornem.) Withers. The maritime form has decumbent-prostrate stems and is late-blooming, whereas the inland form has ascending-erect stems and is relatively early. These differences are of an ecotypic nature. The two forms are ecologically well separated, and natural hybrids are rare (Turrill, 1934). They differ also in several morphological characters. *S. maritima* has green, herbaceous bracts, erect and single flowers, many nonfloriferous, sterile shoots, and a well developed paracorolla inside the throat of the flower. In contrast, *cucubalus* has white, coriaceous bracts, freely flowering stems with well developed inflorescences, nodding flowers, and only a rudimentary paracorolla.

Some taxonomists have fixed their attention on these distinct morphological differences and have named the two as distinct species; others, recognizing their close relationship, have considered them to be subspecies or varieties of one species. The morphological differences between these two forms of *Silene* are of an order similar to the differences between the ecologically distinct subspecies of *Potentilla glandulosa,* and the findings in *Silene* are therefore of significance in relation to those in *Potentilla.*

Artificial hybrids of *Silene maritima* × *cucubalus* are completely fertile, and both the parental forms have $n=12$ pairs of chromosomes. Approximately 200

F_2 hybrids were grown from the cross; they segregated for all the characters that distinguish the parental forms. The F_2 individuals were classified with reference to the parental characters as shown in table 65. The number of plants in this F_2 is small, and estimates of the number and kind of genes that regulate the segregation for each character are uncertain. Moreover, the F_2 individuals were arbitrarily classified into either one or the other parental class. It is clear, however, that the differences between the parental forms are gene-controlled and segregate.

TABLE 65

SEGREGATIONS IN F_2 OF SILENE MARITIMA × S. CUCUBALUS
(AFTER MARSDEN-JONES AND TURRILL, 1928)

F_2 FREQUENCIES

Segregating character	Most similar to: *maritima*	Most similar to: *cucubalus*	Totals
Growth habit	52 prostrate	147 ascending	199
Barren shoots	169 present	30 absent	199
Flowers in inflorescence	86 few	93 many	179
Orientation of flowers	20 erect	109 drooping	129
Petal width	29 wide	107 narrow	136
Paracorolla	29 fully developed	111 trace only and intermediate	140

In this particular cross it seems likely that the difference between the prostrate maritime and the ascending inland habit of growth is controlled by a single pair of genes, and that the ascending habit of the inland form is dominant. The segregations for the other characters suggest, however, that a minimum of two pairs of genes (complementary and oppositional) are responsible for the expression of each character.

GENETIC CONTROL OF MARITIME AND INLAND RACES OF VIOLA TRICOLOR. The otherwise annual *Viola tricolor* has a perennial maritime ecotype growing in sand dunes along the exposed west coast of Jutland, Denmark (Clausen, 1922, 1926, 1951). This maritime ecotype develops many shoots at the ground level during the late fall, in contrast with the inland form of cultivated grass fields, which dies after it has set seeds. The maritime form differs also from the inland in having smaller and thicker leaves, prostrate and darkly anthocyanous stems, and a somewhat later development of flowering. At points in the wild where the two ecotypes meet, no spontaneous hybrids were discovered. A third ecological form of the species occurs inland in coniferous forests on sandy soil. Like the form from the sand dunes, it has a perennial growth habit, but it regenerates less vigorously.

The prostrate habit and the dark purple stems of the maritime ecotype of *Viola tricolor* are both genetically dominant over the erect habit and the green stems of the inland ecotype. Each of these characters is controlled by two pairs of genes having somewhat cumulative effects, and they are not genetically linked (Clausen, 1926). The perennial growth habit of the maritime ecotype is also dominant over the annual, whereas small maritime leaves are recessive to the larger leaves of the inland form. A classification of these last two characters was not attempted, but it was observed that the F_2 segregated in small steps connecting the parental extremes by transitional forms that suggest a multigenic basis.

Genetic mechanisms distinguishing maritime and inland ecotypes of the Madiinae. Several species of the Madiinae, the California tarweeds of the sunflower family, occupy both coastal and inland habitats and have developed parallel pairs of maritime and inland ecotypes. When grown in the Stanford garden between the two Coast Ranges, the maritime race of each species blooms later than the corresponding inland race, and has thicker and more succulent herbage, a lower growth form, and larger heads with more disk and ray florets per head. The reduction in height is achieved in various ways.

In *Hemizonia paniculata* Gray the maritime ecotype has a shorter central stem with denser nodes and more divaricate branches than the inland ecotype. In *Hemizonia multicaulis* Hook. et Arnott, a relative of *H. lutescens* Greene of the hayfield tarweeds of the *Hemizonia congesta* DC. complex, the *multicaulis* race from the exposed Bodega coast north of San Francisco has gone a step farther in low growth by eliminating the central stem entirely and producing only short, divaricate side branches from a central crown.

Layia jonesii Gray, a local endemic from sandy soils near the coast in the vicinity of San Luis Obispo in southern California, has horizontal side branches, but it also retains a short central stem. The highest degree of adjustment in habit form to a windy coast is found in the maritime ecotypes of *Layia platyglossa* F. et M. (Gray) and *Layia chrysanthemoides* (DC.) Gray, which have no central leader but only distinctly horizontal side branches attached to a central crown.

All these differences between maritime and inland ecotypes of the Madiinae are controlled by systems of genes that may vary from population to population. The systems governing segregations for presence and absence of central leader, for horizontal to erect branching, and for late as contrasted with early flowering in *Layia platyglossa* have already been presented in table 63, page 191. The maritime characteristic of late flowering was recessive in all crosses, but horizontal branching and absence of central leader were dominant in certain crossings and recessive in others.

In *Layia chrysanthemoides,* both the horizontal branching and the absence of central leader are recessive in the maritime ecotype with respect to the ascending-erect branches and the presence of central leader in the inland ecotype. An

F_2 population of a cross between the maritime and inland ecotypes of this species consisting of approximately 2000 individuals segregated with respect to the direction of the branches in the ratio of 9 ascending-erect to 7 horizontal (Clausen, 1951, p. 70). This ratio would suggest that two complementary pairs of genes interact to change horizontal branching to ascending-erect. With respect to absence or presence of central leader, the segregation was in the ratio of approximately 13:3, the larger number having a central leader. Such a ratio suggests (1) that the basic recessive biotype has a central leader, (2) that the leader can be suppressed by a dominant inhibitor, and (3) that the inhibitor can be nullified by an epistatic gene for central leader.

Coast Range and Central Valley ecotypes in a weedy bromegrass. That even fairly recent immigrants have evolved distinct ecotypes similar to those of species native to a region is suggested by a study of an annual bromegrass, *Bromus mollis* L., which was introduced into California (Knowles, 1943). This tetraploid species, having 14 pairs of chromosomes, is a native of Europe and especially of the Mediterranean countries. It was not known in California before 1870, but had become common in most regions by 1900. Knowles collected seeds from individual panicles in a range of habitats from Oregon to California and established strains from them in uniform plantings at the University of California at Davis.

The 186 strains grown at Davis fell into two major classes. A late-heading group, requiring 174 to 188 days to head, consisted of 55 strains all from the relatively cool Coastal Transition zone in the outer Coast Ranges from Benton County, Oregon, to Santa Cruz County in central California. An early-heading group, requiring 151 to 164 days, consisted of 131 strains collected from the warmer and drier Lower and Upper Sonoran zones of the valleys and foothills of the inner Coast Range and lower Sierra Nevada of California from Napa County southward to Fresno County. The early group included also 5 strains from southern California, which climatically is similar to the interior central valleys.

It is of special interest that, so short a time after the introduction of a species into a new area, two genetically distinct and thoroughly established ecotypes are found where such ecotypes might be expected. It is not known, however, whether these ecotypes evolved in Europe before their introduction to western North America, or whether they were selected after their introduction. The first alternative seems to be the more probable. The *Bromus mollis* example has some similarity to that of *Capsella bursa-pastoris* already mentioned on pages 171–175, but in *Capsella* the ecotypic situation in Europe is known (Shull, 1937). The *Capsella* forms that grow from Humboldt County, California, northward throughout Oregon belong to the central European, late-blooming ecotype or subspecies, whereas those that occur from Humboldt County southward can be associated with the ecotype native to the Mediterranean countries.

GENETIC CONTROL OF ECOLOGICAL RACES IN GERANIUM ROBERTIANUM. The common cranesbill of the woodlands of northwestern Europe, *Geranium robertianum* L., exists in two major forms, the type form from the woods, and another form native to open, stony beaches (Böcher, 1947). In northwestern Europe both forms are tetraploid, $n=32$ chromosomes, whereas in the Atlantic environment of Great Britain the two corresponding forms are both diploid, having $n=16$ chromosomes (Baker, 1949).

Böcher found that the tetraploid stony-beach type is genetically prostrate and moderately winter-dormant as compared with the erect habit and moderate winter greenness of the tetraploid native to protected woods. The beach form blooms also approximately a month later than the forest ecotype.

The F_1 hybrid between the coastal and forest ecotypes shows hybrid vigor, which is continued in the F_2 generation. Like *Viola tricolor,* but unlike *Silene maritima,* the prostrate growth habit of coastal *Geranium* is strongly dominant over the erect habit of the forest ecotype; even in an F_2 population consisting of 302 plants the erect type was not recovered, 288 of the F_2 plants being completely prostrate, and only 14 having arcuately ascending branches.

This particular F_2 segregation was interpreted to indicate that the prostrate parental stony-beach ecotype has a minimum of four pairs of dominant genes for prostrate growth, P_1 to P_4, and that the erect parental forest ecotype is recessive for all four of them. The class of arcuately ascending F_2 plants was interpreted to be composed of segregants having only one dominant P gene. On a frequency of 256, the ratio would be 247 prostrate to 8 arcuately ascending to 1 erect, or 291.4:9.4:1.2 on the 302 plants of the F_2 population. The significant fact is that, among 302 F_2 plants, there were none of the parental erect type, although the presence of F_2 plants with arcuately ascending branches suggests that the erect condition is being approached.

Another character in *Geranium* also segregated in a ratio that indicates multigenic control. The beach parent had red stems and the forest parent green stems. There were 280 F_2 individuals having green or intermediate stems, whereas only 22 had stems as red as those of the beach ecotype. On the basis of a 15:1 ratio, one would expect 18.8 plants having fully red stems, a good agreement. The green parental forest ecotype, therefore, apparently possessed two pairs of multiple, dominant inhibitors regulating the degree of red color in the stems.

Other segregations for various degrees of winter activity and time of flowering occurred in the *Geranium* cross, but they were not classified. From Böcher's description of the F_2 it is clear that the differences were gene-controlled, and that the variations ranged through gradual steps.

ECOTYPIC SUBSPECIES IN GILIA CAPITATA. The Gilias of the *Gilia capitata* complex of the Polemoniaceae constitute one of the prominent elements of the spring-flowering annuals of California. In the regional floras of California, this complex comprises *G. capitata* Sims, *G. chamissonis* Greene, *G. staminea*

Greene, and *G. abrotanifolia* Nutt. ex Greene. The biologic and evolutionary status of these entities was studied experimentally by V. Grant (1950, 1952). All have 9 pairs of chromosomes, are fully interfertile, and therefore genetically belong to one species, *Gilia capitata* Dougl. Grant treated these groups as subspecies of that species.

Grant's classification of these entities is based primarily on morphology in relation to geographic distribution rather than on the ecotypic responses of plants native to similar kinds of habitat.

Gilia capitata chamissonis is a short-stemmed and low sand-dune form from exposed coasts in central California; in garden cultures it comes into flowering approximately a month later than the tall and early-blooming *Gilia capitata staminea,* which, from its distribution, appears to be an ecotype complex of the interior valleys occurring southward from the latitude of San Francisco. The type subspecies, *Gilia capitata capitata,* is a northern interior form that occupies rocky habitats in the Coast Ranges from San Francisco northward through the state of Washington. It is a tall form, similar to *staminea.* Morphologically distinguishable forms, subspecies *pedemontana* Grant and *mediomontana* Grant, occur respectively in the foothills and at mid-altitudes of the Sierra Nevada up to 2300 m. altitude, but the ecotypic characteristics of these subspecies are not indicated.

Other morphological forms were interpreted by Grant as being recombinations from natural crossings between *chamissonis, staminea,* and *capitata;* they are grouped under the names ssp. *tomentosa* Grant from the coastal region of central California, and ssp. *pacifica* Grant extending from the coastal strip of northern California to the central Oregon coast. Another ecotypic subspecies, *Gilia capitata abrotanifolia,* is found in loose soils of open, sunny hillsides in the foothills of the southern Sierra Nevada and the mountains of southern California, where it occurs up to an altitude of about 2100 m.

All the major ecotypic subspecies of *Gilia capitata* have been intercrossed, but the genetic analysis of the F_2 segregations is based on only small numbers of plants. In the best example, that of ssp. *staminea* × ssp. *chamissonis,* consisting of 212 F_2 plants, the range of variation in time of flowering just barely reached the parental extremes. It is therefore apparent that at least four pairs of genes are responsible for this difference. In ssp. *capitata* × ssp. *chamissonis* the parental types with respect to the width of the corolla lobe were almost recovered among 184 F_2 plants, suggesting that a similar number of genes govern this difference. Among the F_2 progeny of this hybrid there were moderate to strong correlations ($r = 0.16$ to 0.59) among such parental characters as stigma length, color of corolla tube, calyx pubescence, mode of capsule dehiscence, and reflexed calyx lobe. There is therefore a genetic coherence among the characters of the parental subspecies similar to that observed in *Potentilla glandulosa.*

Ecotypes and ecotypic subspecies in Solidago. The genus *Solidago* of the sunflower family has evolved a great many natural races, subspecies, and species in the eastern United States. Many of them hybridize in the wild, so that taxonomically the picture is confused. Some understanding of the biological situation in this complex genus has been obtained through experimental studies on two closely related species, *Solidago sempervirens* L., and its close relative, *S. rugosa* Ait. (Goodwin, 1937*a,* 1937*b,* 1937*c,* 1941, 1944; Charles and Goodwin, 1943).

The seaside goldenrod, *S. sempervirens,* occupies salt marshes, banks of tidal rivers, and sea beaches along the Atlantic coast from Newfoundland to Florida, and farther westward along the Caribbean to Mexico. Three strains from different latitudes and their F_1 and F_2 hybrids were grown at Rochester, New York, at about 43.5° north latitude. The most northern of these strains was transplanted from Ipswich, Massachusetts, at a latitude of 43° N.; at Rochester it had a mean date of first flowers of September 15. Another strain from Ocean City, Maryland, at 38°N., bloomed 2 weeks later, September 28. The third strain came from Fort Myers, in the western part of Florida, at 25°N. The southern strain grew poorly at Rochester, and the few survivors did not begin flowering before November 13, eight weeks later than the Massachusetts strain. The Florida strain was distinctly a short-day form.

When the Florida strain was crossed with the strains from Maryland and Massachusetts, the F_1's were intermediate between the parental races in their time of flowering (Goodwin, 1941, 1944). The F_2's of both hybrids varied between the parental extremes in accordance with a normal binomial curve, and no transgressive segregation was observed. The F_2 populations were small, however, consisting of only 103 and 93 plants, respectively. In the absence of exact data on the parental individuals and of support from F_3's, such populations are insufficient for reliable estimates of the number of genes that segregate.

The genetic analysis of these hybrids nevertheless shows convincingly that the three goldenrod populations represent distinct latitudinal ecotypes of *Solidago sempervirens.* It is equally obvious that the ecotypic differences among these strains are determined by series of predominantly additive genes. The difference between the Maryland and Florida strains in time of flowering is so great that additional latitudinal ecotypes might be expected to exist in the areas between the populations that were sampled.

The inland counterpart of *Solidago sempervirens* is *S. rugosa,* the wrinkle-leaved goldenrod. It is a somewhat weedy species, of dry soil, growing in fields and along roadsides at the same latitudes as the sea-beach goldenrod. Natural hybrids, named *S.* × *asperula* Desf., occur where the inland *S. rugosa* approaches the habitats of *S. sempervirens.* These hybrids are abundantly fertile, and there is evidence of moderate genic introgression between the two.

The many morphological differences between *S. rugosa* and *S. sempervirens* (Goodwin, 1937*a,* 1937*c;* Charles and Goodwin, 1934) include characters that commonly distinguish ecotypes of the same species, such as thicker, more suc-

culent leaves, more pronounced leaf rosettes, more disk florets per head, more contracted inflorescences, and larger seeds in the coastal *sempervirens* as compared with the inland *rugosa* (Goodwin, 1937*c*).

The artificial hybrid between *S. sempervirens* and *S. rugosa* is fully fertile. Each parent has 9 pairs of chromosomes, and the pairing in the F_1 is normal. An F_2 population of 373 plants was apparently as vigorous as the parental species, although rust seemed to be slightly more prevalent on the hybrids than on the parents. The only barriers that separate the inland and the coastal forms are therefore ecological. Biologically, *S. sempervirens* and *S. rugosa* are clearly ecotypic subspecies of one species, despite the many morphological characters that distinguish them. They are comparable with the subspecies of *Potentilla glandulosa* that various authors have named as species.

In the F_2 segregations of these two goldenrods, Charles and Goodwin (1943) showed that some parental characters were correlated whereas others recombined freely. This situation also is similar to the one in *Potentilla.* Goodwin's data do not appear to warrant an estimate of the approximate number of genes that control the differences between the two entities, or of the number of genes they might have in common. His estimates are based on the assumption that all gene differences are of the simple multiple kind with cumulative effects only, an assumption that is highly improbable.

One of the differences between the coastal and inland goldenrods is that the seaside form, *S. sempervirens,* develops large rosette leaves that enlarge one at a time, whereas the inland form, *S. rugosa,* has only short leaves that develop in rapid succession and almost simultaneously. Goodwin (1937*b*) found that the yield of auxin per unit weight of fresh rosette leaf is consistently higher in *S. sempervirens* than in *S. rugosa,* or than in the F_1 hybrid. The higher auxin concentration in *sempervirens* is therefore correlated with a retarding effect on the growth of all but one leaf at a time. These differences in the development of rosette leaves of the two goldenrods appear, then, to be regulated by genes that, in turn, control auxin production.

In conclusion, Goodwin's experiments have shown that the *Solidago sempervirens-rugosa* complex has evolved a coastal and an inland subspecies which are ecologically and morphologically distinct, and that each, in turn, is composed of latitudinal ecotypes. Some of the entities have been recognized as taxonomic species. The differences among them are controlled by systems of genes that produce the effect of blending inheritance.

Ecotypes and geographic subspecies of the Plantago maritima complex. The sea plantains related to *Plantago maritima* of the Plantaginaceae inhabit many kinds of environment around the world. Taxonomically the sea plantains are known under many names. The oldest name in the group is *Plantago maritima* L., and all the entities within the complex have at one time or another been referred to that species. In a narrower sense, however, *P. maritima* refers to the sea plantains of the lowlands of northwestern Europe. Forms from high alti-

tudes in the European Alps are known under the names of *P. alpina* L., *P. serpentina* All., and *P. carinata* Schrad. There has been some uncertainty about the relationship of the sea plantains of the Western Hemisphere. *Plantago juncoides* Lam. was described from Patagonia, but Fernald (1925) identified this form with plants from bluffs and cliffs along both the Pacific and the Atlantic coasts of North America which previously had been referred to *P. maritima*. The salt-marsh form from the eastern United States was classified by Fernald as *P. oliganthos* Roem. et Schult., whereas he listed as a variety of *P. juncoides* the Greenland and Labrador form of the species complex, previously referred to as *P. maritima* var. *glauca* Hornem.

Gregor and associates (Gregor, 1930, 1938, 1939; Gregor, Davey, and Lang, 1936; Davey and Lang, 1939) conducted a most thorough series of investigations on the variations within and between populations of the sea plantains from such diverse parts of the world as northwestern Europe, central Europe, the North Atlantic islands, Iceland, Greenland, and the Atlantic and Pacific shores of North America. These populations from many climates were grown in uniform plots at the station of the Scottish Association for Research in Plant Breeding near Edinburgh, Scotland, and the individual variations of many characters were analyzed statistically in that environment.

Locally, the habitats from which the cultures originated were edaphically distinct, such as coastal marsh, grass meadows above the tide line, coastal cliffs and bluffs, and lowland and alpine habitats away from the coasts. Latitudinally, the sampled habitats ranged from 38° to 70° N.

In both the European and the North American continents the populations of the sea plantains are diploid, having 6 pairs of chromosomes. Most of the central European populations from higher altitudes are also diploid, although some, including the single population of *P. serpentina*, are tetraploid.

Populations originating from edaphically distinct habitats, or from very different latitudes, were found to be distinct for many characters; they represented distinct ecotypes. Besides this interpopulation variation, there was also considerable intrapopulation variability in characters by which taxonomists distinguish taxonomic entities; this finding indicates that such characters cannot be used with confidence in classification (Gregor, 1939). The high-latitude populations from Iceland, and more especially those from Greenland, revealed their ecotypic distinctness through their poor development and high death rate at Edinburgh.

Many of the ecological races were intercrossed, and the fertilities of their F_1's and some F_2 hybrids were noted (Gregor, 1939, table 10). All crossings between diploids were fertile, irrespective of the origin of the forms crossed. Tetraploids crossed with tetraploids were also fully fertile. Second generations were raised from several interecotypic and interregional hybrids between entities that taxonomically have been classified as distinct species. These second-generation hybrids had normal vigor and showed segregations that were of the multiple-

gene type, but the second world war interrupted a detailed statistical analysis of them.

The interregional F_2 hybrids included combinations such as Icelandic with British ecotypes of *P. maritima;* Pacific and Atlantic North American coastal *P. juncoides* crossed with Icelandic and British ecotypes of *P. maritima;* the eastern North American bluff form, *P. juncoides,* crossed with the salt-marsh form from the same coast, *P. oliganthos;* and both of these intercrossed with Swedish *P. maritima.* The findings of both the population studies and the genetic experiments suggest that all the diploid entities biologically belong to one species, *Plantago maritima* L., which evolved many ecotypes and geographic subspecies.

Gregor (1939) found that all the North American forms, including the variety *glauca* from Greenland, are self-compatible and typically have four seeds per capsule, whereas all European forms are self-incompatible wind pollinators and have only two seeds per capsule. The geographic dividing line between these two character combinations runs between the Greenland and Iceland populations of the *Plantago maritima* complex. This line would therefore divide the subspecies *juncoides* from subspecies *maritima.* The F_1's between North American and European *Plantago maritima* have two seeds per capsule, showing dominance of the European parent for this character.

The pattern of distribution and ecotypic differentiation of the *Plantago maritima* complex is an unusual one. This complex has a self-incompatible subspecies in Europe that has evolved edaphic ecotypes along the coasts, lowland and alpine ecotypes in the inland districts, and oceanic island ecotypes in the North Atlantic. In the Western Hemisphere the sea plantains occur in both North and South America, but the Western subspecies is self-compatible and occurs only in a narrow zone along the coasts. On the west coasts of North America only bluff forms of the sea plantains occur, whereas the east coast has both salt-marsh and dry-land ecotypes, together with subarctic to arctic ecotypes from Labrador to Greenland.

The collections and hybrids of ecological races and geographic subspecies from such widely separated habitats provided one of the finest opportunities to analyze the genic control of racial differences in a highly successful organism that probably is evolutionarily old. The sea plantains have preserved their genetic intercompatibility, although those from Europe and from the Pacific coast must have been separated for millions of years.

Ecotypic subspecies within the Armeria maritima complex. The unusual pattern of global distribution and ecotypic differentiation in the sea plantains bears a striking resemblance to that in the sea thrifts of the *Armeria maritima* complex of the Plumbaginaceae (Baker, 1949, 1953). Like the sea plantains, the sea thrifts in Europe have evolved races for salt marsh, for solid ground above the tidal level, for seaside cliffs and bluffs, and for oceanic islands in the North Atlantic. In the Western Hemisphere the sea thrifts occur in southern South

America and along the Pacific coast of North America, where only the bluff and cliff form occurs. Unlike the sea plantains, however, the sea thrifts have no representatives on the east coast of the United States, except that a group of arctic, subarctic, and alpine forms has a circumboreal distribution at high latitudes.

As in the sea plantains, the European races of *Armeria* are cross-pollinating, but they have evolved a structural dimorphism so that pollen from one form can pollinate only the stigmas of the opposite form of the species. The flower heads of these self-incompatible Armerias are colorful and attract insects. The forms from western North America, on the other hand, are monomorphic and self-compatible. They have the stigma type of one of the European dimorphic forms, and the pollen type of the other. Although they do not require cross pollination, they have preserved the conspicuous flower heads of the European forms. The arctic sea plantains are likewise monomorphic and self-fertile, but the corollas are short and the flower heads therefore inconspicuous.

All members of the *Armeria maritima* complex are diploid, having 9 pairs of chromosomes. Taxonomically, some of the central European lowland and alpine forms have been recognized as distinct species, but the remainder of the complex has generally been considered to belong to *Armeria maritima* Willd. (*Statice armeria* L.), with the coastal forms of northwestern Europe representing the type of the species. In Europe, the inland form of the lowlands has been recognized as var. *elongata* Hoffm. The western North American subspecies have been referred to as var. *californica* Lawr. (the southern, smooth-leaf form) and var. *purpurea* Lawr. (the northern form, having ciliate leaves). Likewise, the circumboreal arctic subspecies have been listed as var. *labradorica* Lawr. and var. *sibirica* Lawr. An alpine but morphologically indistinguishable form of the arctic subspecies occurs isolated above tree line in the center of the Rocky Mountains at an altitude of 12,000 feet, 1500 miles from its closest relatives in Labrador and in the Northwest Territory of Canada. This isolated occurrence suggests that during the glacial period the arctic sea thrifts may have had a much wider distribution.

The European, Californian, and arctic subspecies of *Armeria maritima* intercross freely if pollination takes place in the legitimate manner. The California subspecies can be pollinated only by one of the two dimorphic European forms, and its pollen, in turn, is effective only on the opposite European form. The same rule applies to crossing between the arctic and the European subspecies.

It is remarkable that the sea thrifts have conserved full genetic intercompatibility between the inhabitants of the Eastern and Western Hemispheres although they have evolved somewhat different systems of pollination. In parallel kinds of disjunct habitats, they and the sea plantains have evolved parallel ecotypes and ecotypic subspecies. Both groups have their greatest concentration of ecotypes in Europe; in the course of their expanding migration, both developed self-incompatible forms in Europe and self-compatible races in North America and the Arctic.

Altitudinal races in the Mimulus guttatus complex. The common yellow monkey flowers of stream banks, members of the *Mimulus guttatus* complex, have evolved a wide array of ecological races fitting climatic, altitudinal, and seasonal niches in western North America (Clausen, Keck, Hiesey, and Grun, 1949, p. 97; Vickery, 1950, 1951, 1952, 1953). *Mimulus guttatus* Fisch. is tetraploid, having 14 pairs of chromosomes. Its races occupy sites from the immediate coast of the Pacific to stream beds of the high mountain peaks of the Sierra Nevada, and to the floor of the severely continental Great Basin east of the Sierra Nevada. The species has a range from the coast of the Pacific to the Rocky Mountains, and from Alaska to northern Mexico. The related hexaploid complex *M. luteus* L., to which the cultivated *M. tigrinus* belongs, occurs across a similar transect in the South American Andes.

The coastal and the mountain forms of the *Mimulus guttatus* group occurring across the central California transect are strongly perennial, having either long rhizomes or heavy, coralloid horizontal corms. In the vernal stream beds of the interior foothills and valleys, however, are found populations of early-blooming annual races of *M. guttatus,* and populations that consist mainly of annual forms intermixed with a few moderately perennial individuals.

The time of flowering of the climatic races of *M. guttatus* is genetically controlled and differs from race to race. In samples of seedling populations from the central California transect grown in the uniform garden at Stanford, the time of flowering varies from about mid-April to mid-June. The coastal races are late-blooming; those from the interior valleys and foothills are early. The mid-altitude meadow races are the latest, those from slopes at the same altitude being earlier. Unlike *Potentilla glandulosa,* high-altitude races of the *Mimulus guttatus* complex are late-flowering, whereas those from the Great Basin are fairly early.

Nearly all the perennial and annual races of *M. guttatus* are habitual cross pollinators; their anthers do not open until one or two days after the corolla has opened and the stigma has become receptive. Also the anthers are placed below the stigma so that self-pollination cannot take place spontaneously. These races are self-compatible, however, and do not appear to deteriorate after artificial self-pollination. There are at least two normally self-pollinating annual entities which are ephemeral annuals of dry habitats, *M. nasutus* Greene and *M. laciniatus* A. Gray. The anthers of these species empty their pollen directly into the stigma several days before the flowers open. Toward the end of the flowering period, the flowers even become cleistogamous and never open but set viable seed.

Vickery (1952) intercrossed fourteen altitudinal races and subspecies from the central California transect, ranging from the immediate coast to 10,000 feet altitude in the Sierra Nevada, and to the Great Basin. Each strain was crossed in all possible directions. The strains included the two annual species, *M. nasutus* and *M. laciniatus,* and the subalpine to alpine perennial, *M. tilingii* Regel, as well as perennial and annual races of *M. guttatus* in the stricter sense

from various altitudes. Except *M. tilingii,* all these forms are genetically intercompatible, their F_1's being fully fertile, and the F_2's vigorous. Although it is difficult to intercross the alpine *M. tilingii* with races of *M. guttatus,* the F_1 hybrid is fully fertile once it has been produced, and F_2 plants of this combination are as vigorous as the parental species. The barrier against intercrossing is

TABLE 66

INHERITANCE OF ANNUAL AND PERENNIAL GROWTH IN CROSSINGS WITHIN THE MIMULUS GUTTATUS COMPLEX (DATA FROM VICKERY, 1952)

PARENTS, GAMETES, AND F_1 GENOTYPES	F_2 FREQUENCIES		
		Annuals	Perennials
Pescadero *guttatus* × Yosemite Junction (creek) *guttatus,* coastal perennial × foothill annual: $a_1c_1a_2C_2PK \times A_1C_1a_2c_2PK = A_1a_1C_1c_1a_2a_2C_2c_2PPKK$	Obs. . . Calc. . . Ratio . .	84 85.5 9	68 66.5 7
Pescadero *guttatus* × Yosemite Junction (marsh) *guttatus,* coastal perennial × foothill perennial: $a_1c_1a_2C_2PK \times a_1c_1a_2C_2PpKk = a_1a_1c_1c_1a_2a_2C_2C_2PpKk$	Obs. . . Calc. . . Ratio . .	100 93.5 7	115 121.5 9
Pescadero *guttatus* × Dardanelle *laciniatus,* coastal perennial × mid-Sierran annual: $a_1c_1a_2C_2PK \times A_1a_1C_1A_2C_2PK = A_1c_1C_1c_1A_2a_2C_2C_2PPKK$	Obs. . . Calc. . . Ratio . .	724 737.7 57	104 90.3 7
Dardanelle *laciniatus* × Jamesburg *nasutus,* mid-Sierran annual × Coast Range annual: $A_1a_1C_1A_2C_2PK \times A_1C_1a_2C_2Pk = a_1A_1C_1C_1A_2a_2C_2C_2PPKk$	Obs. . . Calc. . . Ratio . .	156 154.5 61	6 7.5 3
Mount Oso *guttatus* × Jamesburg *nasutus,* Inner Coast Range perennial × outer Coast Range annual: $a_1c_1A_2c_2PKk \times A_1C_1a_2C_2Pk = A_1a_1C_1c_1A_2a_2C_2c_2PPKk$	Obs. . . Calc. . . Ratio . .	358 355.5 877	57 59.5 147
Pescadero *guttatus* × Leevining *guttatus,* coastal perennial × Great Basin perennial: $a_1c_1a_2C_2PK \times a_1c_1a_2C_2PK = a_1a_1c_1c_1a_2a_2C_2C_2PPKK$ or $A_1c_1a_2c_2PK$	Obs. . .	0	121

A_1 and A_2: multiple genes controlling annual growth; epistatic over P.
C_1 and C_2: complementary genes which activate the A_1 and A_2 genes, respectively.
P: gene determining perennial growth habit; hypostatic under any of the AC combinations.
K: complementary gene activating the P gene.
Basic recessives, $a_1a_1c_1c_1a_2a_2c_2c_2ppkk$, are annuals.

therefore an initial blocking; once it is overcome, the genes of *guttatus* and *tilingii* are fully interchangeable.

The crossing data thus demonstrate that most of the central California forms of the *Mimulus guttatus* complex constitute one biological species having many ecotypes and several morphologically recognizable subspecies. The two annual self-pollinating entities *M. nasutus* and *M. laciniatus* are morphologically distinct, because each can maintain its own gene pool relatively unmixed. They share with other forms the genes that control annual growth, however.

Table 66 summarizes data on F_2 segregations observed for annual and peren-

nial growth in some of the hybrids of the *M. guttatus* complex. The classification was made in late September after all plants of the annual parental strains had died. The fact that ratios of annuals to perennials varied widely from hybrid to hybrid suggests that the various races contain different kinds of annuals and perennials.

An attempt was made to develop a genetic hypothesis that would account for the observed ratios. Such a hypothesis would have to account for apparent segregation ratios of 9:7 with either the annual or the perennial character as dominant, and for the observation that crossings between the two annuals, *M. nasutus* and *M. laciniatus,* sometimes segregate perennials in the F_2. The proposed hypothesis is highly tentative, especially since no data are available from F_3 and later generations, but is thought to be helpful in attempting to visualize what may be taking place genetically in this species complex.

A system of three pairs of genes, each accompanied by a complementary activating gene, would satisfy the observed segregations, which otherwise would present a confusing picture. Such a theory assumes that the recessive mode of growth in this particular selection of strains is annual, and that the perennial character is determined by a dominant gene, P, with a complementary factor, K. The gene controlling perennial habit, however, is suppressed by the presence of either of two epistatic genes for annual habit, A_1 and A_2, each with its respective complementary gene. The 14 pairs of chromosomes in this species could easily accommodate such a system of six pairs of genes.

The gametic formulas of the parents based on this hypothesis are listed in table 66, together with the zygotic formulas of the F_1 individuals from which F_2's were raised. That most of the parental strains produced some annuals after selfing indicates that they were heterozygous. The annual species of *M. nasutus* and *M. laciniatus,* as well as the vernal creek race of *M. guttatus* from Yosemite Junction, produced only annuals by selfing, but this fact does not exclude the possibility that they are heterozygous for one or several genes.

Besides the strict annuals, there are intermediate forms that are facultative perennials which may regenerate from buds at the ground level without producing rhizomes. The more highly perennial forms among the stream-bank monkey flowers have either strongly developed rhizomes or thickened corms. Genes other than those postulated in table 66 would control such differences between various degrees and kinds of perennials.

The inheritance of earliness of flowering in *Mimulus* as shown by F_2 segregations of many interracial crossings is such that striking transgressive segregation can occur in some combinations. Transgression is especially evident in crossings between parents of highly contrasting origin. The F_2 frequencies in earliness of flowering at Stanford of three hybrid combinations of *Mimulus* are shown in table 67, together with the relative positions of the parental and F_1 individuals for comparison. Segregation is transgressive in the cross between coastal *Mimulus guttatus* and alpine *M. tilingii,* and likewise between the same coastal perennial and mid-altitude annual Sierran *M. laciniatus.* When the same

coastal strain is crossed with a foothill annual race of *M. guttatus,* however, the segregation is not transgressive.

GENETIC AND PHYSIOLOGICAL CHARACTERISTICS OF SPECIES AND ALTITUDINAL RACES OF THE ACHILLEA MILLEFOLIUM COMPLEX. The yarrows, or milfoils, of the genus *Achillea* are among the most successful of wild plants in being able to fit an extremely wide array of climates in the Northern Hemisphere. Extended studies on the composition and growth responses of altitudinal races occurring along the central California transect have been reported in an earlier volume of this series (Clausen, Keck, and Hiesey, 1948). Intra- and interracial physio-

TABLE 67

SEGREGATION FOR DATES OF FIRST FLOWERS AMONG F_2 PROGENIES OF MIMULUS GUTTATUS GROWN AT STANFORD (AFTER VICKERY, 1952)

HYBRID COMBINATION	FREQUENCIES WITHIN CLASSES								TOTALS
	April 9–23	23–May 7	7–21	21–June 4	4–18	18–July 2	2–16	16–30	
Coastal *guttatus* ×				P_1					
alpine *tilingii*	..	59	63	48	*147*	83	11	26	437
				P_2 F_1					
Coastal *guttatus* ×									
mid-Sierran *laciniatus*	3	99	286	*207*	119	28	10	25	777
		F_1		P_2 P_1					
Coastal *guttatus* ×									
foothill *guttatus* (rocky creek)	1	14	*126*	12	...	..	..	..	153
		F_1 P_2		P_1					

P_1, P_2, and F_1 indicate the relative position of the parents and the F_1.
Class of median frequency is italicized.

logical differences were studied in controlled environments by Hiesey (1953*b*). More recent work (Ehrendorfer, 1952, 1953; Clausen, Hiesey, and Nobs, 1955) has clarified the relationships between the North American and the European members of this complex, and has contributed new information on the genetic structure of this diverse group, although these investigations are still incomplete.

Preliminary studies by Ehrendorfer indicate that in central Europe there are at least three morphologically distinctive diploid species, having 9 pairs of chromosomes, that are ecologically separated. They include *A. tomentosa* L. of dry slopes in southern Europe, *A. asplenifolia* Vent. of moist saline places in the Pannonic steppe, and *A. setacea* Waldst. et Kit. of dry sand steppes. A tetraploid species, *A. collina* Becker, grows at fairly low altitudes under dry and warm conditions. The hexaploid *A. millefolium* occurs at higher altitudes and in moister habitats but extends also to northern Europe, where it is found in the

lowlands in Scandinavia and Iceland. Another hexaploid species, *A. stricta* Schl., occurs at higher altitudes in woods in central Europe. Finally, an octoploid with 36 pairs of chromosomes and referable to *A. pannonica* Scheele occurs on rocky steppes at low altitudes; morphologically it resembles the tetraploid *A. collina.*

In North America there is a west coast and oceanic hexaploid species, *A. borealis* Bong., and a more continental tetraploid species, *A. lanulosa* Nutt. (Lawrence, 1947). Later investigations (Ehrendorfer, 1952) have disclosed the existence of evolutionarily significant islands of the tetraploid species within the area of the west coast hexaploid, including salt-marsh habitats of the San Francisco Bay region, areas in the moist redwood region of northern California and adjacent coastal Oregon, and the Olympic Peninsula of the state of Washington. In both central Europe and western North America the species having polyploid chromosome numbers appear to merge into one another morphologically.

Among the diploid species there seem to be strong barriers to the interchange of genes, for hybrids between *A. setacea* and *A. asplenifolia* and between *A. asplenifolia* and *A. tomentosa* are sterile (Clausen, Hiesey, and Nobs, 1955). On the polyploid level, however, morphologically and ecologically contrasting forms having the same chromosome number intercross freely, and F_1 hybrids are fertile although individuals of the same F_1 combination may vary in the percentage of good seed after either self- or open pollination.

Hybrids between contrasting ecological races within either the tetraploid *borealis* or the hexaploid *lanulosa* of North America are often more vigorous than the parents, and this hybrid vigor is carried into the F_2 (Nobs, Clausen, and Hiesey, 1953). Both morphological and physiological characters segregate widely.

The relation of hybrid vigor to the environment is illustrated by the hexaploid interracial cross between *Achillea borealis* ssp. *gigantea,* from the hot Central Valley of California at 34° N., and *A. borealis,* from the cool North Pacific Kiska Island at 52° N. (Clausen, Hiesey, and Nobs, 1951). The California valley race is a giant form having deep taproots able to penetrate to underground water levels during rainless summer periods. It is winter-active at Stanford but is especially adapted for growth at higher day and night temperatures (Hiesey, 1953*b*). In contrast, the Kiska race is a subarctic dwarf having long, slender, shallow rhizomes suited to conditions of the wet, cool tundra of its native habitat. At Stanford this race retains its dwarf habit and winter dormancy, but nevertheless flowers nearly 2 months earlier than the more slowly developing valley race. The F_2's from this hybrid are spectacularly variable (Hiesey and Nobs, 1952), recombining characters that are of significance in the ecologic adjustment of the parental races to their respective native environments.

In the lowland garden at Stanford the vigor of the F_2 plants ranges between that of the parents. At the mid-altitude garden at Mather, however, to which a sample of 300 F_2 cloned individuals was transplanted, the vigor of the F_2 is highly transgressive (Clausen, Hiesey, and Nobs, 1954). At Mather both paren-

tal races are near their limit of survival, but for different reasons. The Central Valley race grows well during the warm summers at Mather, but is weakened and eventually dies because of the relatively severe winters. The reverse is true of the strain from Kiska Island, which survives the winters but is weakened during the warm, dry summers. The F_1 and more than 90 per cent of the F_2 progeny survive in this same environment with vigor far transcending that of the parents. Further studies on the responses of this highly segregating F_2 population at the three altitudinal stations, Stanford, Mather, and Timberline, are still in progress.

Other F_2 populations involving interecotypic crosses at both the tetraploid and hexaploid levels of the *millefolium* complex grown at Stanford show complex segregations in morphological characters. Attempts to resolve the inheritance of these characters in terms of genic formulas would, however, be futile in view of the complexity introduced by polyploidy superimposed upon a probable multiple-gene type of inheritance governing the various character differences.

Seasonal ecotypes within Lamium purpureum. The red deadnettle, *Lamium purpureum* L., of the mint family, is a small, weedy annual of cultivated fields throughout Europe, which probably in prehistoric times was introduced with cultivated plants from western Asia. The species contains both a winter-annual and a vernal ecological race, and the two are adjusted for development in different seasons (Müntzing, 1932). In Scandinavia the vernal or summer-annual race germinates in the early spring, blooms the same summer, and thereafter dies, whereas the winter-annual race germinates in the fall, blooms the following spring, and then dies. The winter-annual race does not flower before it has lived through a winter season, and if it is sown in the spring, it does not flower until the spring of the following year.

At Lund, Sweden, Bernström (1953) tested the flowering responses of twenty-eight populations of *Lamium* from various geographic sources by growing them as summer annuals that were sown in the spring. Fourteen responded like the vernal race and flowered within 4 to 6 weeks after sowing. The other fourteen developed vegetatively and either flowered late during the fall and then only sparsely, or did not flower at all. The latter group was, therefore, developmentally a variable one that contained several kinds of biotype, but the composition of this group was not analyzed further. The strains of the vernal race originated from continental environments in central and northern Europe having cold winters, whereas those of the nonvernal group were from more southern habitats having milder winters.

Müntzing crossed the vernal and the winter-annual races, obtaining an intermediate F_1 which produced many seeds, but many did not germinate; consequently the second generation consisted of only 30 plants. Conspicuous variation among the F_2 was noted, but no tabulation was attempted because of the small number of plants.

Seasonal dimorphism has also been reported in *Lamium intermedium* Fr., in

L. amplexicaule L., and in *L. hybridum* Vill. *Lamium purpureum* and *L. amplexicaule* are diploids with 9 pairs of chromosomes each, and *L. intermedium* and *hybridum* are both tetraploid, having 18 pairs of chromosomes. In *L. intermedium,* leaves having the appearance of forma *vernale* develop on plants that germinate in the fall; they differ from the leaves of forma *aestivale,* which come from plants that have germinated in the spring. Müntzing (1932) found that the seasonal dimorphism in *L. intermedium* was due to environmental modification, and not to genetic differences as in *L. purpureum*. Seeds harvested on *L. intermedium* f. *aestivale* in the late summer and sown in the fall germinated immediately; the seedlings survived the winter, developed into the morphological forma *vernale,* and bloomed in the spring. The seeds of forma *vernale* harvested in May and sown in May germinated also immediately, developed into forma *aestivale,* and came into bloom 6 weeks after sowing. Both forms die after flowering once.

Within *Lamium amplexicaule* Bernström (1952) found that thirteen strains ranging in origin from Syria and Sicily to Sweden were all summer annuals, blooming a few weeks after being sown in the spring. He also found, however, that six strains from Hungary, southern Russia, Turkey, and Egypt apparently were winter annuals, so that this species, like *L. purpureum,* has also evolved genetically distinct races having two kinds of periodicity.

In summary, the annual species of *Lamium* exist over a considerable range of latitude, and have been able to evolve hereditarily distinct races for distinct seasons. Some races of certain species are specialized and can utilize only the summer or the winter-to-spring season, but others are more tolerant and can utilize either.

Inheritance of the annual and biennial character in Melilotus. The white sweet clover of the pea family, *Melilotus alba* Desr., normally a biennial species, flowers only infrequently during its first year of growth, but during that period develops a central stem and vigorous side branches. After one winter the central stem dies, and side shoots which flower freely develop from the dense leaf axils of the thickened root crown.

Melilotus alba seems to have originated in western Asia, but during the past four or five centuries it has invaded western Europe and has spread from there to North America and Australia. Another biennial form of this species was introduced to South Dakota from northern Siberia about 1915 under the name *M. suaveolens*. Unlike the type of *M. alba,* the *suaveolens* form has yellow flowers, but the two forms are genetically fully intercompatible.

An annual form of *M. alba* was discovered in Alabama of the southeastern United States and was brought to general attention in 1917 by H. D. Hughes, of Iowa State College. Botanically this new variety was named var. *annua* Coe (Pieters and Kephard, 1921). Studies by Castetter (1925) and Hugh Smith (1927) indicate that the new annual variety and the biennial form both are diploid, having 8 pairs of chromosomes. Agronomically, the annual variety is

known as the variety Hubama of white sweet clover; unlike the normal form of the species it blossoms freely on the dominant primary stem during the first year, has no thickened root crown, does not tiller from the top of the crown, and dies after the first season.

Castetter (1925) reported that the biennial form does not flower even during the second season if it has been kept inside a heated greenhouse during the winter; if kept outdoors over winter, however, it flowers. In contrast, the annual form will die if left outside during winter, but will continue growth and reproduction indefinitely if kept under warm conditions. Castetter emphasized that "thus *Melilotus alba* has two functionally distinct types."

The genetic differences between the annual and biennial forms were investigated by Hugh Smith (1927), who found that both forms were self-compatible although the flowers have to be "tripped" in order to effect pollination. The flowers are normally bee-pollinated, and spontaneous crossing is common. If grown adjacent, the annual and biennial forms cross spontaneously.

Individuals of the biennial white sweet clover transplanted to a field were emasculated and artificially pollinated by pollen of the annual form. The ensuing F_1 plants were self-pollinated by tripping. The number of seeds obtained per plant was relatively small, however, and the sizes of the individual F_2 progenies ranged between 4 and 53 individuals.

From 91 F_1 individuals, 2032 F_2 plants were obtained and were tabulated with respect to their biennial or annual character. All the F_2's were lumped together in the final tabulation, yielding a total of 1563 biennials to 469 annuals. Calculated on a 3:1 ratio, the expectancy is 1529:503, a deficiency of only 34 individuals in the recessive group. However, the ratios of the progenies from the individual F_1 plants were highly variable, for in 6 progenies added together there were 173 biennials to 10 annuals, and among 17 other F_2 progenies there were 170 biennials to 158 annuals. The first group is close to a 15:1 ratio; the latter approaches a 9:7 ratio.

In the absence of more critical data, conclusive evidence cannot be obtained about the kind of gene system that governs this ecologically significant difference. The evidence suggests that the difference is controlled by more than one gene, and that multiple and complementary genes may be involved in some of the progenies. The theory that the annual form arose by a simple recessive mutation in one of the southern states is probably oversimplified. It seems more likely that, when the original biennial forms arrived in North America from the Old World, variation existed for some of the underlying genes controlling periodicity. When combinations of genes giving rise to the annual habit appeared in the more northern environments, selection would favor the preservation of the biennial type, but in one of the southern states, the annual form was favored.

The two types of *Melilotus alba* parallel the differences between the winter-annual and vernal ecotypes of *Lamium purpureum,* and represent a pattern found within many other species and also between closely related species. Such forms are of the kind that may be differentially selected in distinct climates.

Seasonal and climatic races in the Madiinae. Species that occupy both the Mediterranean-type winter rain regions and the cooler temperate latitudes have often evolved seasonal races similar to the winter-annual and vernal races in *Lamium purpureum*. Which of the two kinds will be selected in either of the two regions may depend upon the ecologic-physiologic make-up of the species. In *Lamium purpureum* the races are short-lived and utilize either the winter season only, or the spring and early summer. In *Melilotus alba* the forms are longer-lived than the *Lamium,* and survive normally for at least one year.

Several of the annual species of California tarweeds of the subtribe *Madiinae* of the sunflower family have evolved races for distinct seasons. All the species of the Madiinae germinate during the late fall after the rains start, and live through the mild California winter, but some may flower in the early spring, others during the summer, and still others during the fall. When sown in a warm greenhouse, they flower without winter chilling. The periodicity of these races of annuals therefore consists in an adjustment to the season when they become mature for flowering rather than an adjustment to the season during which they are able to germinate.

Babcock and Hall (1924, pp. 51–54) recognized that various tarweed species possessed seasonal ecologic races and discovered that these differences were gene-controlled. In the section *Euhemizonia* of the genus *Hemizonia,* Babcock and Hall recognized that the April-blooming *H. citrina* Greene is a spring-flowering form of the otherwise fall-blooming (August to September) *H. lutescens* Greene, and that *H. rudis* Benth. is a fall-blooming form of the normally spring-flowering *H. luzulaefolia* DC. The white-flowered species *H. luzulaefolia* occurs in a geographical area south of the yellow-flowering *H. lutescens;* the spring- and fall-blooming forms of each species, however, occur within their respective territories, or even in the same neighborhood (Babcock and Hall, 1924, p. 54). In both species, which in Babcock and Hall are treated as subspecies of *H. congesta* DC., the vernal race is of short stature and has large stem leaves and few glands, whereas the autumnal race has taller stems, much reduced stem leaves, and highly glandular foliage. The vernal races of these species remain alive almost until autumn in irrigated garden plots at Stanford, but they retain their morphological distinctness from the autumnal races beside them. In their native habitats, however, the vernal races die at the beginning of the dry season.

The genetically best-known example of seasonal periodicity in the Madiinae is *Madia elegans* Don. The formulas for the system of oppositional genes that regulate the time of flowering in a vernal and autumnal race of this species were presented in table 64, page 193. Actually, there are three seasonal races in *Madia elegans.* Two occur at lower altitudes, namely, a vernal race, *vernalis,* and an autumnal race, ssp. *densifolia* (Greene) Keck. Both germinate during the late fall and occur in interspersed colonies through the Coast Ranges, valleys, and foothills of California, but the vernal and autumnal races come into evidence at different seasons. A third race, *aestivalis,* occurs in California as a mid-altitude

mountain ecotype that flowers during the summer. Morphologically it is intermediate between the vernal and autumnal races.

The vernal and autumnal races of *M. elegans* are developmentally and morphologically distinct. The vernal race does not develop a conspicuous basal leaf rosette, but begins elongating the internodes even during the cool winter. It has only a few inconspicuous glands, and is branched all the way from the base. Possibly all the populations of the vernal race possess the principal gene controlling early flowering, E, although they range in time of flowering, from population to population, from mid-March to late May.

The autumnal race, on the other hand, develops only a dense leaf rosette during the late winter and cool spring. During the warm, dry summer months of June and July, however, it develops tall, stout stems densely clothed with heavily glandular leaves, and it branches only from near the summit of the stem. Possibly all populations of the autumnal race are recessive, ee, for the gene controlling earliness, but local populations vary in height and range in time of flowering from mid-June to late August, and probably therefore have different numbers of the genes L_1 and L_2 controlling lateness of flowering.

The montane summer race appears to be both a seasonal and an altitudinal ecotype. It blooms at midsummer, is branched from the base, is glandular, and is not densely clothed with stem leaves.

Vernal and autumnal ecotypes have likewise been found within the 6-chromosome *Holocarpha obconica* (Cl. et Keck) of the *Holocarpha virgata* complex, formerly considered to be members of the genus *Hemizonia* (Clausen, 1951). The differences between the two seasonal ecotypes of this *Holocarpha* species are much the same as those between the vernal and autumnal ecotypes of *Madia elegans*. The vernal form branches from the base and has almost no glands, whereas the autumnal ecotype is much taller, is branched only at the summit of the main stem, and is densely clothed with heavily glandular leaves. In garden cultures under irrigation, however, the vernal ecotype of *Madia elegans* dies early, whereas the corresponding vernal ecotype of *Holocarpha obconica* survives until autumn and becomes heavily glandular as the summer progresses. It nevertheless remains distinct from the autumnal ecotype in its lower stature, more diffuse branching, and its ability to begin flowering in March and to continue until late in the season. The autumnal ecotype does not begin to flower until late in July.

In the wild, the spring ecotype of *Holocarpha obconica* dies when the dry season begins. Here it is so distinct morphologically from the autumnal ecotype that when first discovered it was thought to be a distinct species, and was described as *Hemizonia vernalis* (Keck, 1935). It is known from two localities, each population of which has 6 pairs of chromosomes. These can be crossed with the most distinct population of the autumnal ecotype (Clausen, 1951, fig. 42, p. 103). The F_1's are fertile and produce vigorous F_2's that segregate for growth habit and time of flowering, proving the genetic control of the racial differences.

Even the genera of the Madiinae as such show differential seasonal adjustments. All the species of the genus *Layia* are early-blooming annuals that complete their growth cycle before the end of May. They are plants with succulent, mesic herbage that escape the dry period. In the genus *Madia* one group of species is composed of spring-blooming annuals that die at the onset of the dry season; another group consists primarily of summer-blooming species. The diploid *Madia elegans* ($n=8$) has spring-, summer-, and fall-blooming ecotypes, and the tetraploid *M. sativa* Mol. ($n=16$) has summer- and fall-blooming races that parallel those in *M. elegans*.

Most of the tarweeds of the genus *Hemizonia* are summer- to fall-blooming species. The early spring leaves of this genus are large, soft, and mesic, but the leaves developed later become xeric. In the hayfield tarweeds of the section *Euhemizonia* the stem leaves become reduced in size, highly glandular, and pubescent. In the spikeweeds of the section *Centromadia,* on the other hand, the summer and fall stem leaves are reduced to spines. Certain species in these two sections have evolved both vernal and autumnal ecotypes.

The ecological differentiation found between races of some of the most successful species of the Madiinae may therefore also be reflected in the ecological pattern of the genera and subgenera of the subtribe as a whole. The intraspecific differences are especially interesting because they are amenable to genetic analysis, and foreshadow what may have occurred in previous geologic ages before the genera differentiated.

The California tarweeds are annuals that live at moderately low altitudes in a region having a mild and moist winter-to-spring season, followed by a hot and dry summer-to-fall season. In such a region the climate in spring is radically different from that of the summer and fall. The tarweeds are essentially winter annuals without chilling requirements; such plants would be expected to flower during the spring and to set mature fruit and die before the arrival of the dry season. Most tarweeds, however, have been able to make the remarkable adjustment in morphology and physiology that enables them to begin their major growth period when grasses and most annuals become summer-dormant, leaving the California oak savannas open to the summer- and fall-flowering tarweeds.

GENETIC-PHYSIOLOGIC CONTROL OF PERIODICITY IN LOLIUM. The ryegrasses of the genus *Lolium* form a group of closely related species or ecological races of annuals and perennials. Recent studies by Cooper and Saeed (1949) and by Cooper (1950, 1951, 1952, 1954) on the interrelations between heredity and environment in the control of seasonal and flowering responses in contrasting races and species of *Lolium* have thrown new light on the inheritance of physiological characteristics of climatic races.

A complex of forms of ryegrass is included under the names *Lolium perenne* L., *L. italicum* Braun, and *L. rigidum* Gaud. These and other species of *Lolium* are all diploid with 7 pairs of chromosomes, are freely intercrossable and fairly interfertile, and biologically may be considered to be one polymorphic species

complex (Jenkin and Thomas, 1938). All these forms outcross by wind pollination. Among the most contrasting of the races of this group are early-flowering, nontillering annuals which occur in the Mediterranean region, as compared with late-flowering, freely tillering perennials grown extensively in the colder and more humid climates of northwestern Europe as hay and pasture grasses. These extreme forms are connected by many kinds and recombinations of intermediates.

The annual forms include races commonly designated as *L. italicum* and *L. rigidum,* and are well suited to warm, arid climates such as are found in southern Europe, New Zealand, and Australia. When sown in spring they normally head freely and thus complete their normal life cycle during the same season.

By contrast, the perennial forms, which include various races of *L. perenne,* are unable to flower unless they are first subjected to a period of cool temperatures and short days followed by a period of longer days and warm temperatures. The required conditions for flowering in perennial ryegrasses are normally satisfied if they are sown outdoors in the autumn, exposed to the cool temperatures and short days of winter, and then to the increasingly longer and warmer days of spring and summer.

The physiological steps leading to flowering are complex and still largely unknown (cf. Murneek and Whyte, 1948; Anton Lang, 1952), but in *Lolium,* as in other plants, at least three fairly well defined stages can be recognized that can be studied more or less independently: (1) ripeness to flower (the "Blühreife" state of Klebs, 1918, or "competence" of Cooper); (2) initiation of flower primordia in the inflorescence; and (3) elongation and differentiation of the inflorescence. In the perennial forms of *Lolium* exposure to cold is required for the attainment of stage 1, ripeness to flower, but the annual forms of *Lolium* do not require cold treatment. The photoperiod is a conspicuous environmental factor governing the attainment of stage 2, initiation of floral primordia. All forms of *Lolium* require minimum day lengths ranging from 9 to 14 hours, depending on the strain and species; the annuals are generally earlier, and are activated by a threshold of shorter days than the perennials. Longer photoperiods ranging up to continuous illumination may accelerate the development of stage 2 in any of the forms. The final stage, 3, elongation of the inflorescence, is favored by high temperature after the flower primordia have been developed.

Cooper's studies on the inheritance of the differences in flowering characteristics of contrasting strains were directed primarily to a study of factors controlling stages 1 and 2. He crossed Wimmera ryegrass, an annual form of *Lolium rigidum* developed at the Waite Agricultural Research Institute, Adelaide, Australia, and S. 23, a late-flowering, prostrate perennial pasture type of *L. perenne* selected at Aberstwyth, Wales (Cooper, 1954). These two parental forms represent approximately the extreme contrasts within this complex of cultivated ryegrass. The hybrid progeny of this cross were tested in three environments chosen to disclose differences in requirements for vernalizing cold treament and for photoperiod.

The environments were the following: (1) a heated greenhouse kept above 10° C. with continuous light, providing a test of ability to flower without previous cold treatment; (2) vernalization by exposure to a temperature of 3° C. for 6 weeks, followed by transfer to the heated greenhouse with continuous light, a test for ability to flower after cold treatment; and (3) sowing outdoors February 27, exposing the seedlings to slight vernalization and to the natural day-length period, providing a test of capacity to flower when exposed to continually increasing photoperiods. The tests in the three environments were made simultaneously on seedling samples of 5 to 30 individuals of the parental populations, on 33 to 65 individuals of the F_1, and on samples of 97 to 186 F_2 individuals. The F_2 populations were obtained by mutually pollinating three modal F_2 individuals.

The plants fell into two major categories: those that headed and therefore had reached ripeness to flower, and those that remained nonfloriferous. The plants of the first group were subclassified according to the number of leaves produced before flowering. The point where flower buds were initiated varied between leaf number 4 and leaf number 27, counting from the base.

In the first environment, the heated greenhouse with continuous light, the *perenne* parental race remained uniformly vegetative, and all 30 plants of the *rigidum* parent flowered, although the inception of the heading in different plants varied from leaf number 4 to number 21. Twelve of 33 F_1's and 17 of 97 F_2's were nonheading, and in both generations the variation in inception of heading ranged between leaf numbers 12 and 30. In progeny from the backcross between the F_1 and the *rigidum* parental strain, all 18 plants flowered, whereas 5 of 10 progeny resulting from backcrossing to *perenne* were nonflowering; among those that flowered, heading was initiated at higher nodes than in progeny from the backcross to *rigidum*.

In the second environment (vernalization by 6 weeks' cold treatment at 3° C. followed by continuous light in the heated greenhouse), the 20 plants of the parental *rigidum* strain headed uniformly at leaf numbers 4 to 6, in contrast with the great range of variation of this same strain in the nonvernalized condition. The cold treatment therefore affected even this strictly annual strain by inducing heading at a lower node. The 19 seedlings of the parental *perenne* strain were only partly vernalized by the cold treatment, for only 9 plants headed, at leaf nodes that ranged between 14 and 27 as compared with nodes 4 to 6 in *rigidum*. More than 50 per cent of the *perenne* seedlings were nonheading under this treatment. The partially nonheading response of the *perenne* seedlings is significant, because 170 F_2 seedlings and 18 backcross progeny from the $F_1 \times$ *L. perenne* all headed. The cold treatment was therefore sufficient to vernalize all the hybrid progeny, but it did not vernalize a portion of the *perenne* parental population.

The frequencies in the progenies and parental strains of heading versus nonheading plants, the essentially symmetrical distribution of the F_2 individuals in regard to the node where heading occurs, and the position of the means in rela-

tion to the frequency curve suggest the kind of genetic system that operates in the second environment. It appears that a series of additive genes are responsible for the differences in floral responses of Wimmera ryegrass, of S. 23, and of the F_2 plants. In the absence of F_3's, however, the F_2 and backcross progenies are too small to estimate the number of genes that control this particular set of responses, although it probably is less than ten.

The third environment, in which samples of these cultures were sown outdoors in early spring and exposed to increasing lengths of the natural photoperiod, served as a reference point for the two semicontrolled situations. The responses outdoors were intermediate to those in the two indoor environments.

Within selected cultivated strains of both annual *L. rigidum* and perennial *L. perenne* there is sufficient residual genetic variability to make it possible to select forms that differ in their flowering characteristics when they are grown in environments for which they have not been selected. Wimmera ryegrass, for example, when grown under continuous light in a warm greenhouse, segregates seedlings differing considerably in earliness. By mutually pollinating the four earliest individuals and also the four latest, Cooper was able to develop two progenies that in a warm greenhouse under continuous light differed significantly in their earliness. Outdoors the same progenies appeared to be identical with respect to flowering. The genetic variability inherent in the population of Wimmera ryegrass was concealed by the preconditioning during the winter period, which was sufficient to induce heading in all the genotypes.

Even greater residual genetic variability was found to be carried by individuals of *Lolium perenne.* Tests were made on the selfed progeny from three apparently similar individual plants of the early-flowering S. 24 form of *perenne,* and also on the three progenies that resulted from diallel crossings between them. Seed samples from these six progenies were grown under three different conditions, as follows: (1) sown outdoors in autumn under natural day length (the conditions under which the parental populations had been selected for uniformity); (2) sown outdoors in autumn, but exposed to a shorter photoperiod of 9 hours (a critical period designed to reveal differences between early- and late-flowering fractions); and (3) sown in spring outdoors under natural photoperiod (designed to test capacity to flower without prior cold treatment).

Under the first treatment, flowering was essentially uniform in all six progenies, and they were indistinguishable. Under treatment 2, all the progenies, both those from selfing and those from crossing, were resolved into a flowering and a nonflowering group, and wide ranges of variation in earliness were observed among the flowering groups. Within the nonflowering groups, a fraction was found in which spikelets were initiated but failed to elongate, and a second fraction in which the plants remained completely vegetative.

Under the third treatment, spring sowing outdoors, one of the selfed progenies yielded only nonflowering individuals, the typical response of *Lolium perenne;* another selfed progeny yielded 14.3 per cent flowering plants, whereas nearly all the progeny of the third selfed plant flowered. All the hybrids from the diallel

crossing yielded both flowering and nonflowering plants, the relative proportions between the two groups being related to the genotypes of the parental individuals.

The genetic variation governing flowering responses within the outcrossing species *Lolium rigidum* and *L. perenne* is in contrast with the genetic uniformity of inbred self-pollinating species such as *Lolium temulentum*. Two progenies from single plants of *temulentum* subjected to the same series of treatments as in *L. perenne* failed to show appreciable variability. In the outbreeding strains of ryegrass, however, the genetic composition is such that populations consisting of relatively few individuals are capable of preserving systems of genes that control hidden variability even after rigid selection for agronomic types has taken place. Such "spare" genes may under proper environmental conditions express a high degree of phenotypic diversity.

Genetic-physiologic control of flowering in Sorghum. In milo, a grain type of *Sorghum vulgare,* multigenic control of the maturity stage for flowering ("ripeness to flower") has been established by Quinby and Karper (1945) in studies based on F_1, F_2, and F_3 progenies. The date of first flowers in the various milo strains closely parallels the dates when the floral primordia are formed.

Sorghum vulgare Pers. (*Holcus sorghum* L.) is an old cultivated crop plant originating in tropical Africa. Older theories, cited by Arber (1934), assumed that the annual *Sorghum vulgare* had its origin in wild forms of the rhizomatous perennial western Asiatic *Sorghum halepense* (L.) Pers., also known as Johnson grass. Huskins and Smith (1932), however, point out that this oft-repeated theory, which stems from E. Haeckel, is based on a misinterpretation of Haeckel's statement. He placed both the annual and perennial Sorghums in one vast species, *Andropogon sorghum,* and emphasized that certain central African annual forms were possibly the progenitors of the cultivated Sorghums, but the inclusion of the wild annuals with the perennials in a single species was merely a matter of taxonomic convenience.

Chromosomal investigations (Huskins and Smith, 1932, 1934; Karper and Chisholm, 1935; Garber, 1944, 1950) have shown that all the annuals of the *Sorghum vulgare* complex have 10 pairs of chromosomes, and that the perennial *S. halepense* has 20 pairs. The 10-paired forms that have been investigated include the cultivated forms of milo, kafir corn, feteria, kaoliang, durra, sorgo, broomcorn, Sudangrass (*S. sudanense*), and many wild forms from Africa taxonomically referred to as *S. virgatus* Stapf (Tunis grass), *S. verticilliflorum* Stapf (Tabucki grass), *S. effusus* Stapf (Kameroon grass), *S. drummondii* Hack., *S. laewisooni* (Piper), *S. vogelinanum, S. lanceolatum, S. arundinaceum, S. guineense, S. margaritiferum, S. caudatum, S. subglabrescens, S. cernuum,* and others.

Considering the highly distinct forms that exist within the cultivated sector of *Sorghum vulgare,* Huskins and Smith and also Garber emphasized that the 10-chromosome wild relatives justifiably could be included within *S. vulgare.* Quinby and Karper, and likewise Garber, also found that the 10-paired culti-

vated wild Sorghum forms of the *Eusorghum* section or subgenus are genetically completely intercompatible. It therefore seems reasonable that the wild 10-chromosome "species" of the *S. vulgare* complex represent ecotypes some of which furnished the original gene pool giving rise to the cultivated Sorghums.

Sorghum halepense, or Johnson grass, occurs at warm-temperate latitudes in western Asia; it is also a member of the subgenus *Eusorghum.* Besides having twice as many chromosomes, it differs from *S. vulgare* in having creeping, scaly rhizomes that make it perennial and a troublesome weed. Genetically Johnson grass is fairly incompatible with the cultivated Sorghums. Artificial F_1's are highly sterile, but, from spontaneous hybrids that have passed through several generations, fertile strains can be recovered, as, for example, Johnsorgo, which, like Johnson grass, has 20 pairs of chromosomes (Karper and Chisholm, 1935). Johnsorgo has absorbed some characteristics of *S. vulgare,* however, for its rhizomes are shorter than those of Johnson grass and it is less perennial.

The species of the neighboring section or subgenus *Parasorghum* are genetically much more widely separated from one another than those of *Eusorghum.* Garber (1950) and Karper and Chisholm (1935) found that various forms of the African *S. versicolor* and *S. purpureo-sericeum* have only 5 pairs of chromosomes, and Australian species of *Parasorghum* have 10 pairs. Garber found that intraspecific hybrids among 5-paired species were successful, but no hybrids were obtained in crossings between species. Moreover, the 5-chromosome species failed to cross with 10-chromosome species of *Parasorghum.*

In an attempted intersectional crossing between the Australian 10-chromosome *Sorghum nitidum* of *Parasorghum* and *S. vulgare* of *Eusorghum,* only 12 seeds were obtained from 170 florets; only 1 of these germinated, and this proved to be a selfed plant of *S. nitidum.* The strong genetic isolation between species of *Parasorghum* is in marked contrast with the high genetic compatibility within the subgenus *Eusorghum.* It seems unlikely, therefore, that any of the African *Parasorghum* species entered into the origin of the cultivated Sorghums.

The origin of the many cultivated forms of *Sorghum vulgare* is lost in the antiquity of primitive man. In Arber's book (1934) is reproduced a carved relief from the palace of king Sennacherib, Nineveh, dating from about 700 B.C., depicting a sow with its litter of piglets near a well kept field of giant *Sorghum.* In the United States various introduced strains of *Sorghum vulgare* have been grown almost continuously since about 1860 (Martin, 1936; Karper and Quinby, 1946, 1947). It is evident that much elimination of biotypes through selection must have taken place since the crop was introduced. Sorghum strains directly introduced from tropical Africa to warm-temperate latitudes may grow to giant heights within a few months, but they bloom too late in the season, or fail to flower altogether.

Through gradual selection, strains of this tropical grass have been developed that are able to bloom successfully under temperate conditions. In the United States the culture extends northward to 54° latitude, and in altitude to 1600 m. on the Colorado plateau. The commonly cultivated strains of Sorghum are now

very uniform. A factor contributing to the uniformity has been the circumstance that, although occasional crossing by wind pollination occurs, these strains are predominantly self-pollinated.

The loss of variability during the process of climatic and agronomic selection of the cultivated Sorghums may have resulted in a simpler genetic composition than they had before their introduction into agriculture. In 1945, Quinby and Karper reported that at that time only two maturity types were grown in the United States, the others having been eliminated. The late and ultralate varieties went out of culture about 1900. A great change has taken place in the crop with respect to the period required for maturity. Quinby and Karper used strains which were able to start flowering within 2, 2½, or 3 months, respectively, after sowing when planted at Lubbock, Texas, at a latitude of 34° N. and an altitude of 1060 m.

Quinby and Karper (1945) intercrossed two types of milo, the variety Sooner, flowering at Lubbock within about 60 days, and the variety Dwarf Yellow of intermediate earliness, flowering in about 80 days. The F_1 hybrid was ultralate, requiring 100 to 114 days and being a month later than the latest parent. The F_2 progeny segregated in the ratio of 9 ultralate to 3 intermediate to 4 early. This ratio was explained by assuming that the intermediate Dwarf Yellow parent, $Ma_1Ma_1ma_2ma_2$, possessed a basic gene, Ma_1, for late blooming that was lacking in the Sooner parent, $ma_1ma_1Ma_2Ma_2$. The latter, on the other hand, possessed the intensifier, Ma_2, whose effect was to make Ma_1 even later, but its presence cannot be detected in the absence of Ma_1.

The correctness of the theory was adequately tested by studying 159 F_3 progenies from as many selfed F_2 plants. The F_3 segregations indicated that 88 F_2 plants belonged to the transgressive ultralate phenotype Ma_1Ma_2; 30 to the intermediate parental Ma_1ma_2; and 39 were early, being recessively $ma_1ma_1 \cdot \cdot$. The calculated frequencies are very close to the observed, namely 89.5 : 29.8 : 39.7, a total of 159.

It was found that besides these two genes for maturity there is a third, Ma_3, which apparently is a multiple of Ma_2; it can express itself only in the presence of Ma_1, but its effect is less than that of Ma_2 and not additive to it. The Ma_3 gene is fairly closely linked with the recessive counterpart, r, of the gene R for plant color. Likewise, Ma_1 is closely linked with the recessive gene dw_2 causing short nodes. These linkages of genes having a physiological effect with genes controlling morphological differences aid in the interpretation of the data.

At Chillicothe, Texas, which is at the same latitude as Lubbock, but at an altitude of only 500 m., the mean minimum and mean maximum temperatures during June and July are approximately 3° and 1.5° C higher, respectively. The same biotypes that were grown at Lubbock were also sown at Chillicothe. Under these circumstances the periods required for initiation of flowering of the three maturity types were shortened, being 48, 66, and 102 days, respectively. At considerably higher latitudes and altitudes, as in eastern Colorado at about 1600 m., having colder nights, those varieties that are very sensitive to photoperiod be-

come large and productive, whereas at Chillicothe such varieties mature quickly and make little growth.

The Ma_1 gene can express itself only at certain levels of photoperiod. In a cross between the triple recessive Early Sooner, $ma_1ma_2ma_3$, and the intermediate Dwarf Milo, $Ma_1ma_2ma_3$, segregating for the Ma_1ma_1 gene only, approximately equal samples of the F_2 plants were grown under different lengths of day. One sample of 67 F_2 plants was grown under a short day of 10 hours, and a similar sample of 69 plants under the natural day length at Chillicothe of approximately 14 hours in midsummer. At the 10-hour day both parents came into bloom 46 days after planting, and the 67 F_2 plants flowered uniformly early, ranging between 42 and 56 days. At 14 hours, however, the early parent bloomed after 56 days, and the intermediate after 78 days. Distinct bimodal frequencies could be observed among the 69 F_2's: one group of 17 plants corresponded to the early parent, and another group of 52 plants was in the class with the intermediate parent. The frequencies in the two classes represented a ratio of 1:3. Long days, which are atypical for this tropical species, activated the Ma_1 gene for delayed flowering and brought to expression the difference between the two genotypes, Ma_1 and ma_1.

Variation in height of the plants and length of leaves follows the variation in earliness. At the natural 14-hour midsummer photoperiod at Chillicothe, the number of days required for the initiation of flowering in the various biotypes was as follows: for the early, $ma_1Ma_2ma_3$, 48.6 ± 0.3 days; for the intermediate, $Ma_1ma_2ma_3$, 68.6 ± 0.4 days; for the late, $Ma_1ma_2Ma_3$, 82.6 ± 0.7 days; and for the ultralate, $Ma_1Ma_2ma_3$, 102.4 ± 0.4 days. In height, the corresponding biotypes reached 85.8, 87.7, 121.6, and 151.8 cm., respectively, and in leaf length, 54.8, 65.1, 65.3, and 78.1 cm. The three genes regulating maturity are therefore also genes that influence other characters of the plant.

At a day length of 10 hours the number of leaves produced before heading was 12.2 to 12.6 in all four biotypes listed above, but at the 14-hour period, the numbers were 16, 22, 23.5, and 31.5 leaves, respectively. This variation in number of leaves before heading parallels the same kind of variation in *Lolium* in different environments.

The length of the internodes between leaves is also influenced by the four maturation types. The internodes of early ma_1 strains increase in length from the ground level to the inflorescence; in contrast, the intermediate $Ma_1ma_2ma_3$ strains have a short internode at the top, and decrease in internodal length downward; the late, $Ma_1ma_2Ma_3$, and the ultralate biotypes, $Ma_1Ma_2\cdot$, have short internodes both close to the ground and near the inflorescence.

The three pairs of maturity genes are therefore key genes of extreme ecological significance in determining the latitudes for which the plants are best suited, and they also determine their general vigor. These genes probably represent only parts of a much more complex system that would be discovered if strains directly from the tropics could be intercrossed with strains selected at the outer margins of the area tolerated by the species. The genes that have proved

to be so significant for their success in North America apparently would not be expressed at latitudes near the equator, and were probably suppressed by epistatic genes when the species was first brought to temperate latitudes. It is a fortunate circumstance that a genetic analysis as thorough as the one by Quinby and Karper could be conducted in a region where these three pairs of genes could come to full expression.

Ecological differentiation within apomictic Poas. Predominantly asexual apomictic species have evolved genetic systems capable of ecological adjustments that are as effective as those of normal sexually reproducing species. The bluegrasses of the genus *Poa,* which set their functional seed mostly without fertilization, have been eminently successful in developing genetically distinct forms fitted to almost all available ecological niches at latitudes ranging from arctic to warm temperate. In doing so they have evolved distinct ecotypes that differ physiologically (Hiesey, 1953*a*), but the genetic mechanisms that have given rise to them are of a different order from those of sexual species.

The sexual process still functions to some degree in most apomictic plants that reproduce primarily asexually. An equilibrium exists between seeds originating by apomictic cloning and those developed by the usual sexual method (Clausen, 1954*b*). In partially apomictic strains, the progeny from apomictic seed is normally of greater vigor than progeny produced by the sexual process, which are therefore mostly eliminated through competition and often are not even observed. The sexual mechanism is nevertheless of evolutionary significance, because it provides some opportunity for the apomictic strain to hybridize. New apomictic lines having new recombinations of characters may thus arise within one or two generations.

In apomictic species ecological races may differ from one another in large blocks of chromosome complements, in contrast with sexual species, in which finely balanced systems of genes are selected for different ecological niches. The mechanism of apomixis makes it possible for distinct species to exchange sets of chromosomes without many of the hazards that make exchange between genetically well separated sexual species highly perilous for the progeny, largely because, in apomixis, constancy in sexual reproduction is not necessary for success.

The Poas are for the most part species of cool or cold environments. They cluster at high latitudes in both the Northern and Southern Hemispheres, and at lower latitudes they occur mostly on the higher mountain ranges. The geographic distribution of the Poas is in contrast with that of the species of *Lolium,* which center in the warm-temperate region around the Mediterranean and have been able to gain a foothold in the milder parts of the cool-temperate region. *Poa* is also in contrast with *Sorghum vulgare,* a tropical species which, being an annual, has been able to evolve genetic races able to survive in areas of the warm-temperate zone having warm summers.

Hundreds of *Poa* species have been described and grouped under sections of this genus, but their relationships appear to be reticulate. Only two sections of

the genus will be considered here. The basic chromosome number is 7, and many species have multiples of 7. Most of the apomictic species are high polyploids, and many have an uneven number of sets, or sometimes broken sets (Hartung, 1946).

Western North America is the home of approximately 15 to 18 species of perennial bunchgrasses that appear to belong to a large and as yet unrecognized section of *Poa*. In the taxonomic classification by Hitchcock (1950), the species of this section would include all of *Scabrellae* and *Nevadenses,* and parts of the *Alpinae* and *Epiles*. The species of this section inhabit areas ranging from mild coastal winter-rain regions to alpine areas at altitudes as high as 4000 m.

Another section of the genus includes rhizome-bearing sod grasses of the *Pratenses,* to which belong the circumboreal *Poa pratensis* L. and *Poa arida* Vasey of the North American prairies, and also possibly a few other species. *Poa pratensis* in western North America has evolved many native forms for most of the same climatic zones occupied by the bunchgrass section, but the *Pratenses* grow primarily in moist meadows, whereas the bunchgrasses occur mostly on open, dry slopes. Hitchcock includes a series of dioecious species within the *Pratenses* section, such as *P. nervosa* (Hook.) Vasey, *P. arachnifera* Torr., and the three dune species, *P. macrantha, P. douglasii* Nees, and *P. confinis* Vasey, which possibly are related to the South American section *Dioicapoa*.

The bunchgrass section contains a series of 12-ploid apomictic *Poa* species, having $2n=$ca. 84 chromosomes. Along the central California transect from the coast to middle altitudes in the Sierra Nevada, *Poa scabrella* (Thurb.) Benth. is common. Within this area at least three ecotypes can be distinguished. At Stanford all three are active during the cool, moist winter and spring, and become dormant during the dry summer. The mid-altitude race from 1400 m. in its native habitat is forced into both winter and summer dormancy, its entire growth period being compressed between early April and mid-June; nevertheless, it is able to persist as a successful perennial. At Stanford it dies after a short period.

Above 1800 m. in the Sierra Nevada, *P. scabrella* is replaced by *P. gracillima* Vasey and *P. canbyi* (Scribn.) Piper. Both these grasses are winter-dormant and summer-active, even when transplanted to a mild and moist winter region. The alpine altitudes are occupied by the tiny, tufted *Poa rupicola* Nash. Farther north, in Oregon and Washington, *P. gracillima* remains in the mountains, *P. canbyi* becomes a spring and early summer grass at moderate altitudes east of the Cascades, and the 84-chromosome Sandberg bluegrass, *Poa secunda* Presl., is a vernal species of drier habitats and somewhat lower altitudes.

In the Pacific Northwest there is another group of bunchgrass Poas that have mostly $2n=63$ chromosomes, an unbalanced complement of 9 sets of 7 chromosomes each. The group includes *Poa ampla* Merr., the big bluegrass, and *P. nevadensis* Vasey, a meadow grass from altitudes above 1000 m. Both are species that occur on the continental side of the Cascades and the Sierra Nevada. At least three ecologically distinct races of *Poa ampla* are known: one is from the

lower Columbia River plains at 200 to 500 m. altitude; another race from 600 to 1000 m. is adjusted to the rich, deep loess of the Palouse Prairie and to the somewhat colder climate; the third is a subalpine race occurring between 2600 and 3000 m. in altitude in the Rocky Mountains. The last has $2n=84$ chromosomes and is unable to survive in the lowland garden at Stanford, but is successful at Timberline. The races of *Poa ampla* from lower altitudes remain green during the winter in their native environments, and are winter-active at Stanford. Another form of the *Poa ampla* complex, which occurs on alkaline flats in the Great Basin, is known under the name of *Poa juncifolia* Scribn.

The bunchgrass Poas have evolved species and races fitting most of the environmental niches in the western half of the United States, some being adjusted to one season, and others to other seasons. Local and unnamed apomictic strains combine morphological characters of several of the species mentioned above.

The most widespread species complex of the bluegrasses is *Poa pratensis* L., or Kentucky bluegrass. It is circumboreal, and occupies altitudinal zones from sea level to almost 4000 m. and habitats varying from moist meadows to gravelly or sandy slopes. In steppe regions it may be found at moderately high altitudes. The forms of this complex are known under various names: *P. angustifolia* L., *P. irrigata* Lindm., *P. alpigena* (Fr.) Lindm., and *P. arctica* R. Br.

Various forms of Kentucky bluegrass span the Northern Hemisphere from the northernmost places inhabited by plants southward at least to latitude 34° N. Thorild Wulff (Ostenfeld, 1923) reported *Poa arctica* common and flowering along the north coast of Greenland at 83° 6′ N., only 765 km. from the North Pole. Farther south at subarctic latitudes it merges into subspecies *alpigena* and *irrigata,* and finally through them into *Poa pratensis* proper.

Under natural conditions *Poa pratensis,* unlike most other Poas, may have almost any number of chromosomes from approximately $2n=38$ to $2n=150$. "Haploid" and subhaploid forms having $2n=36$ and 18 chromosomes, respectively, arose from a plant having $2n=76$ and retained fertility (Kiellander, 1942). Löve (1952) found in Iceland plants of subspecies *irrigata* with chromosome numbers ranging from $2n=82$ to $2n=147$ chromosomes. Within an area with a diameter of 10 m., Löve found plants having $2n=82$, 84, 87, 91, 95, 98, 105, 108, 111, 112, 113, and 119 chromosomes, yet there was a tendency for plants having a higher number of chromosomes to occur at higher altitudes.

In subspecies *arctica,* Nygren (1950) found $2n=39$ chromosomes in an isolated southern colony at Dovre Mountains in Norway, and $2n=56$ to 88 in forms from mountains in northernmost Sweden. Likewise, in subspecies *alpigena* he found individuals ranging in chromosome number from $2n=48$ to 92. In an *alpigena* plant having $2n=73$ chromosomes he observed in pollen mother cells a distribution to daughter nuclei of 26, 28, 30, 34, 35, 37, 38, 39, 41, and 42 chromosomes per cell.

In the Sierra Nevada of California various biotypes of apomictic *Poa pratensis* may grow intermingled in the same meadow. In a sample of 12 plants from

near Mather at 1400 m. altitude all were found to be biotypically distinct from one another, differing in habit, stature, color of herbage, susceptibility to disease, and time of flowering. Apomictic as well as sexual species may therefore consist of local populations having a wide mixture of biotypes.

Hybridizations by Müntzing (1940), Åkerberg (1942), and the Carnegie Institution group (Clausen, Keck, and Hiesey, 1947*b*; Clausen, Grun, Nygren, and Nobs, 1951; Grun, 1952, 1954, 1955) have shown that the chromosome number varies greatly after crossing, and that *Poa pratensis* crosses successfully with *Poa alpina* L. in northern Scandinavia, with the almost ephemeral bunchgrass *Poa scabrella* in California, and with *Poa ampla* on the Palouse Prairie of Washington. In second-generation progeny of some of these hybrids, new combinations may be produced that fall taxonomically within *Poa pratensis.* These may become apomictic and, although having many characteristics of *P. pratensis,* may display physiological and morphological characteristics from the other parent species as well (Hiesey, 1953*a*). These facts suggest ways in which the great diversity within the *pratensis* complex may have arisen in the wild. Chromosome numbers of successful hybrid lines may show great variation in the process of adjustment; not infrequently they gain or lose as many as 30 chromosomes in a single generation (Triplett and Clausen, 1954; Cox and Clausen, 1955).

During the migration of *Poa pratensis* around the world it evidently has been able to hybridize with many species from many climates, and to absorb heredities from them. In doing so, its forms have acquired tolerances to unusual ranges of environment. The *pratensis* forms, however, have been able to preserve a coherent and genetically penetrating combination of morphological characteristics that identify the group as a natural taxonomic entity: the long rhizomes, the typical dense pubescence on the lower half of the lemma, and a characteristic shape of the inflorescence. It seems likely that selective processes operate to favor this combination even though forms of *Poa pratensis* from various parts of the world may vary considerably. On a somewhat smaller scale a parallel evolutionary situation exists in the equally apomictic grass *Calamagrostis purpurea* L. (Nygren, 1951).

GENETIC SYSTEMS DIFFERENTIATING SUBSPECIES AND OTHER TAXONOMIC ENTITIES IN PLANTS

As can be deduced from some of the previous examples, ecological characteristics may differentiate not only the ecotypes, but also morphologically distinct subspecies of a species, ecospecies of a species complex, and distinct though related genera. In the pages to follow, examples of genetic systems that control the characters of taxonomic entities will be reviewed. These examples suggest patterns through which evolutionary processes may have proceeded at the higher levels of taxonomic differentiation.

Inheritance in the Geum urbanum-rivale complex. *Geum urbanum* L., the common avens, is a plant of the rose family native to wooded slopes, and *G. ri-*

vale L., the water avens, is morphologically a different species of neighboring moist meadows. The two hybridize spontaneously at their points of contact, and the hybrids are fertile, yet the adjacent parental forms do not lose their identity. This situation in certain respects parallels that of the slope subspecies *reflexa* and the meadow form *hanseni* of the distant relative *Potentilla glandulosa.*

Natural hybrids between the two *Geum* species have been recognized for a long time, having been described by Schiede (*Plantae hybridae,* p. 72, 1825) as *Geum urbano-rivale.* The hybrids are commonly referred to as *G. intermedium* Ehrh. Lange (1856–1859) described a colony of the intermediate form in Denmark occurring between the slope and the meadow forms along the "Princess path" at Sorgenfri near Lyngby, in the outskirts of Copenhagen. This same locality was studied by Öjvind Winge and Jens Clausen in 1925. The *urbanum* form still occurred on the wooded slope, *rivale* in the boggy meadow below, and a few intermediate hybrids of slightly variable combinations were found alongside the pedestrian path in the narrow contact zone between the two.

A morphological comparison of the populations of the parental forms indicated that they were somewhat variable, like most average populations of these species, but no evidence of introgression was found, and no extensive recombinations of the characters of the parental species such as were known in experimental F_2 populations growing in the near-by experimental field. The *rivale* form flowered earlier than *urbanum,* as Lange had noted 75 years earlier.

Gajewski (1950) also reported on the rarity of this hybrid in the Bialowieza National Forest in Poland. He found the parental species adjacent, but separated by a forest road. He suggested that *Geum urbanum* follows man, and that the hybrids are a by-product of man's activity. Not only were hybrids rare, but no generations later than the F_1 were found.

Geum urbanum has green herbage; small, narrow, yellow petals; erect flowers; and sessile fruits. *G. rivale,* on the other hand, has dark, reddish herbage; larger and wider rose-colored petals with traces of yellow; strongly nodding flowers; and fruits separated from the calyx and the petals by a short piece of stem, a gynophore.

In world distribution, *G. urbanum* is Eurasiatic, extending eastward to the Himalayas. It occurs mainly south of latitude 60° N. and at lower altitudes except in the Mediterranean zone, where it is montane. *G. rivale,* in contrast, extends north of the Arctic Circle in Scandinavia, and is both Eurasiatic and eastern American; toward the south it tends to occupy altitudes above those of *urbanum,* and occurs as high as 2400 m.

The distribution patterns of the two forms emphasize their different ranges of tolerance, although they overlap in central Europe. Where their ranges overlap, they are isolated edaphically, and in part also temporally. The moist-meadow form *rivale* appears on the whole to have a greater tolerance to cold, and the *urbanum* slope form a greater tolerance to heat, just like their counterparts in the two subspecies of *Potentilla glandulosa.*

Gärtner (1849) produced artificial hybrids between *G. urbanum* and *G. rivale,*

finding the F_1 to be fertile and intermediate. The F_1 progeny of one cross *G. urbanum* × *G. rivale* was variable, some individuals approaching *rivale* and a few, having yellow flowers, approaching *urbanum*. After backcrossing the hybrid *G. urbanum* × *G. rivale* with pollen of *G. rivale* for four generations, Gärtner was able to produce a strain similar to *G. rivale* but having *urbanum* cytoplasm, an early example of "introgressive" hybridization. Focke (1881), citing this example, points out how fallacious it is to assume that those natural hybrids that in appearance approach *G. rivale* should have been obtained on *rivale* as the maternal parent, or that those favoring *urbanum* should be the reciprocal combination of *G. urbanum* × *G. rivale*.

This cross has been repeated many times, but F_2 progenies have usually been too small to contribute to an understanding of the mode of inheritance of characters distinguishing these species. Both species are hexaploid, having $2n=21$ pairs of chromosomes, three times as many as in *Potentilla glandulosa*. The chromosomes pair as regularly in F_1 plants as in nonhybrids. The hybrids can be selfed, and are genetically completely compatible; F_2 segregations are complex, and the more extreme variants are rare. Many of the potential recombination types have probably never been seen.

Winge (1926, 1938) grew 2000 F_2 plants resulting from the selfing of 6 F_1 individuals and reported (1926, p. 595) that some of these progenies favored *urbanum*, others *rivale*, and that still others were intermediate. The two parental individuals were apparently heterozygous for certain hidden genes which came to expression in F_2 recombinations after crossing. The parental individuals came from the two adjacent populations near Lyngby, mentioned above.

In backcrosses of F_1 to *G. urbanum*, Winge found that the progeny superficially resembled *G. urbanum*; likewise, in backcrosses to *G. rivale*, the progeny were apparently similar to *rivale*, although closer inspection revealed some interspecific variation in the progenies. Winge pointed out that on account of the relative rarity of the hybrids, and the overwhelming frequency of individuals of the parental forms, the F_1 or later generations would largely be backcrossed to the two parents. He also emphasized that the complex genetic system is bound to 21 pairs of chromosomes. At any one time, therefore, only an infinitesimal fraction of the heredity of one species would be transferred to the population of the other, although the cumulative effects of thousands of years of interbreeding should not be ignored. Natural selection apparently is strong enough to keep the two ecologically contrasting species distinct.

Details of the segregation in Winge's cross have never been published. Fortunately, another paper by Prywer (1932) contains a careful analysis of the segregations of 20 characters in the F_2 of a cross *Geum urbanum* × *G. rivale*, the parent strains of which came from the vicinity of Warsaw, Poland. The F_1 consisted of 100 individuals, and the F_2 of 1000, only 550 individuals of which were classified. Many of the segregating characters were parallel to those in *Potentilla*, such as height of plant, length of leaves, date of first flowers, and color of petals.

In Prywer's parental *Geum rivale* the petal color was cream with light red veins in contrast with rose petal color in Winge's *rivale*. Both investigators used a form of *urbanum* having lemon yellow flowers. The F_1 in Prywer's cross was reported to have petals of the same color as in the *urbanum* parent. In the F_2 the segregation was transgressive, ranging from deep yellow (apparently lemon chrome) at one extreme, to white petals at the other. This similarity to the segregation in *Potentilla glandulosa* suggests that Prywer's *Geum rivale* possessed a gene for lemon chrome that was suppressed by whitening genes.

One character showed distinct monogenic inheritance in both Winge's and Prywer's crosses, namely anthocyanin coloration in stems and petals of *G. rivale* as compared with green stems in *G. urbanum*. Prywer found 395 anthocyanous to 122 green among 517 F_2 plants (theoretically 387.7 : 129.3). Winge obtained the ratios 3 : 1 in F_2, and 1 : 1 in backcrossing to *urbanum*.

Like the forms of *Potentilla glandulosa,* the common avens and the water avens have not acquired full specieshood; they are morphologically well defined ecological subspecies that are separated partly in the time of flowering, but genetically are wholly interfertile. This example emphasizes the point that a strong ecological barrier can override a strong genetic affinity.

A cross between *Geum rivale* and a third member of this hexaploid complex, *G. coccineum* Sibth. et Sm., was analyzed by Gajewski (1950). *G. coccineum* is a species with large, showy flowers of alpine meadows in the mountains of the Balkan Peninsula and in Asia Minor. It rarely occurs with *G. rivale,* but where it does, natural hybrid populations are formed which are referable in the taxonomic literature to *G. jankae* G. Beck.

The hybrid *G. coccineum* × *G. rivale* is fully fertile, and the chromosome pairing is normal. The segregating taxonomic characters in the F_2 parallel those of the *urbanum-rivale* hybrid, and also those of the subspecific hybrids of *Potentilla glandulosa*. The orientation of the sepals, for example, differs in the parents from reflexed in *coccineum* to erect in *rivale,* and the orientation of the petals likewise is horizontal in *coccineum* and erect in *rivale*. In an F_2 of 192 plants the segregation was of the multiple genic type with some skewness; the most frequent class of F_2 plants was the one having horizontal sepals and horizontal petals.

With respect to the width of the petals, the *rivale* parental strain had petals 6–10 mm. wide, and *coccineum* 12–27 mm. The petals of the F_1 were intermediate, 10–14 mm., but among 182 F_2 plants petal width ranged from 6 to 20 mm. Backcross individuals to *rivale* varied between 6 and 12 mm., whereas backcrosses to *coccineum* had a range of 11–17 mm., both of which are fairly similar to the ranges within the parental strains. The multiple genes that control petal width would appear to be of the additive kind, but only data from F_3's could determine whether the apparent binomial regularity in distribution in the F_2 was caused by genes of additive effect only, or by a blend of genes of additive, subtractive, and complementary effects.

In the inheritance of petal color there was a clear complementary effect. The

rivale parent was cream-colored, and *coccineum* deep orange-red; the F_1 was clear yellow. Apparently in the F_1 the red element in the *coccineum* color was inhibited by something coming from the cream-colored *rivale*. Among 299 F_2 plants, 169 were of the clear yellow type, 62 were orange to red, and 68 were cream. This ratio is very close to 9 : 3 : 4 and suggests a difference in two pairs of genes, but the segregation is difficult to visualize on the basis of the action of two genes.

Such a segregation could be expected, however, if orange-red *coccineum* has a dominant gene for yellow and one for red, and if cream *rivale* has a dominant suppressor for red but none of the genes of *coccineum* for yellow and red. The F_1 would then be yellow, YyRrSs. In the F_2 one would expect a segregation in the ratio of 39 yellow YRS + Yrr·· to 9 orange YRss + 3 red yyRss to 13 cream yyRS + yyrrss. Among 299 F_2 individuals, the calculated frequencies would be 182.8 yellow : 56.2 orange to red : 60.0 cream to white, a moderately good agreement with the observed frequencies. Gajewski mentions that there were many differences in intensities and shades between the colors that could not be classified. These gradations suggest the presence of additional modifying genes; they would account for the variations in the shades of reddish and cream, and for some of the difficulty encountered in classifying the F_2.

Like *Geum urbanum,* alpine *G. coccineum* has green, nonanthocyanous herbage. In the F_2 progeny of *G. coccineum* × *G. rivale typicum,* Gajewski found 78 anthocyanous and 29 green individuals among a total of 107. This is close to the 3 : 1 ratio of 80.3 : 26.7, and parallels Winge's and Prywer's findings in the cross *Geum urbanum* × *G. rivale.* Moreover, in crossing the green *Geum rivale pallidum* with anthocyanous *G. rivale typicum,* Gajewski obtained 60 anthocyanous to 19 green (theoretically 59.93 : 19.7). Also, Dahlgren (1924) obtained in a cross between Swedish forms of these two subspecies of *G. rivale* 391 anthocyanous *rivale* to 137 green *pallidum* (theoretically, 396.0 : 132.0). In view of the multiple genic control of most characters in the *Geum urbanum-rivale-coccineum* complex, it is of interest to find one character that has a one-gene control. This simple control has been verified by three independent investigations in five crossings involving four taxonomic entities in three countries.

Geum coccineum, like *G. urbanum,* has no gynophore, whereas in parental *G. rivale* Gajewski measured gynophores ranging between 4 and 11 mm., with a mean of 7 mm. Only 2 among 83 F_1 plants had gynophores, and these were in the range between 1 and 2 mm. Among 297 F_2 plants, the length of the gynophores ranged only between 0 and 5 mm., with 166 individuals in the 0–1 mm. class, and only 9 F_2 plants in the 4–5 mm. class. Even among 102 backcross individuals to the recessive *rivale* parent, having a long gynophore, only 2 individuals were in the class of *rivale*. These findings suggest that in *G. coccineum* about five to six pairs of suppressors prevent the development of the stipe between the calyx and the fruit-bearing receptacle. The class frequencies indicate that some of the suppressors are dominant or epistatic. Plants with gynophores comparable with those of *rivale* were segregated as rarely in the F_2's and back-

crosses of Winge's *urbanum* × *rivale* hybrids as in the *coccineum* × *rivale* combination.

In contrast with *Potentilla glandulosa,* species of the genus *Geum* have very long and elaborate styles, which can be looped or straight, smooth or feathery. In *G. coccineum* and *rivale* and other species of the section *Eugeum,* the lower part of the style is separated from the upper by a semiloop; the portion below the loop hardens and dries, and the upper end detaches, leaving a hooked rostrum on the dried fruit. The hook serves as an attachment organ to seed-transporting animals, including man. Various elaborations on this structure from species to species of *Geum* serve as morphological markers aiding taxonomists in distinguishing species.

In *Geum coccineum* the rostrum that ends in the hook is smooth and about 3.5 mm. long. In *G. rivale,* however, both the rostrum and the detaching tail are strongly ciliate, and the hooked rostrum is 7–11 mm. long, with a mean of 9.1 mm. In the F_1 the rostrum is moderately ciliate, but only 3.5 mm. long, the same as in *coccineum.* In 182 F_2 plants the rostrum varied in length between 1 and 9 mm., having a mean of 4.5, and in 113 backcross individuals to the recessive *rivale,* the range was 2 to 11 mm., with a mean of 5.5. In the backcross there were 13 individuals in the 7–11 mm. *rivale* classes. The inheritance of length of the rostrum suggests control by a series of perhaps three or four multiple genes of which at least one has an epistatic, dominant, shortening effect. In addition, other genes control the amount of ciliation or hairiness on the rostrum and on the detachable tail.

The morphological characters that separate *Geum rivale, G. urbanum,* and *G. coccineum* are of the kind that in other plant families are of primary taxonomic significance, and that separate species or even distinct genera. In *Geum* they are controlled by systems of multiple genes, but recombinations of these do not result in gross physiological unfitness although obviously there is a high correlation between the morphological character and the fitness of the species to the particular environmental conditions. In a biosystematic sense these morphological characters serve as markers of ecologically separated subspecies rather than as markers of distinct species. Some taxonomists may prefer simply to refer to them as species, however.

Geum rivale itself is a complex of ecotypes of moist meadows. On the Scandinavian Peninsula, Turesson (1925) recognized experimentally a lowland, a subalpine, and an alpine ecotype of this species, and was aware of the existence of additional ecotypes in other areas. *Geum urbanum* is its counterpart from dry, somewhat shaded slopes. The horizontal and altitudinal range of *urbanum* would suggest that it, too, may be composed of several ecotypes. The alpine meadow form, *Geum coccineum,* is probably more homogeneous ecologically. Irrespective of their intraecological differentiation, each of these three entities maintains a different gene pool that enables it to fit its specific edaphic niche within a broad climatic zone. These three major gene pools are conveniently marked by distinct morphological characters.

The *Geum urbanum-rivale-coccineum* complex is unique within the genus in its absence of genetic barriers. Gajewski (1948, 1949, 1950, 1953, 1954, 1955) reported on diallel crossings between 13 species within the *Eugeum* subgenus or section, all having 21 pairs of chromosomes, and found that most of these interspecific hybrids were highly sterile, producing no progeny. A few hybrids, however, were only partially sterile. The Russian avens, *G. aleppicum* Jacq., and *G. molle* Vis. et Panc. apparently also belong to the *urbanum-rivale* complex in a wider sense. With *G. rivale* and *G. urbanum* these species yield hybrids that are 10 to 25 per cent fertile.

Another complex of *Eugeum* consists of *Geum macrophyllum* Willd., its subspecies *perincisum* (Rydb.) Fern., and *G. oregonense* Rydb. Hybrids between these show perfect chromosomal pairing, but are only 32 to 46 per cent fertile. Crosses between the *urbanum* and *macrophyllum* complexes, however, are sterile. In the F_1 hybrids between *G. macrophyllum* and *rivale* and *G. urbanum,* little or no pairing between the 42 chromosomes of the hybrids is found, and the latter of the two F_1 hybrids is sublethal. The F_1 hybrid *G. macrophyllum* × *G. aleppicum* is reported to have approximately 21 pairs of chromosomes, to be sublethal, and to have deformed flowers. With such a high chromosome number the possibility exists, however, that some of the pairing is autosyndetic.

Within the subgenus *Eugeum* there are also 10-ploid and 12-ploid species having 35 and 42 pairs of chromosomes (Gajewski, 1949). No species of this subgenus having 28 pairs, and none having lower numbers than 21, have been discovered. The F_1 hybrids between 21-chromosome *G. rivale* and the 35-paired *G. quellyon* Sw. or the 42-paired *G. pyrenaicum* Willd. were found by Gajewski (1949) to have approximately 21 pairs of chromosomes, leaving respectively 14 and 21 chromosomes unpaired. This observation suggests that these polyploid species of *Eugeum* have the same basic three sets of chromosomes as found in *G. rivale.*

Related to the species of *Eugeum* is a group of montane species that variously have been referred to the genus *Sieversia* or have been included as a distinct subgenus or section within the genus *Geum*. These species have long, straight, and pinnately pubescent styles similar to those of the related high arctic or high-montane genus *Dryas,* or of the montane genus *Chamaebatia* of the Sierra Nevada. Seeds of this type are carried by wind rather than on the fur of animals.

Within the *Sieversia* group at least three chromosomal levels are represented, namely, $n = 14$, 21, and 35 chromosomes (Gajewski, 1952). The tetraploid *Geum montanum* L. ($n = 14$) ranges from the subalpine zone up to about 2300 m. altitude from Spain to the Carpathians and Balkans. The hexaploid *G. reptans* L. occurs from 1700 to 2700 m. in the alpine zone of the Alps and Tatra, and also in the Balkan mountains. The dekaploid 35-chromosome *G. bulgaricum* Panc. is another local alpine of the Balkan Peninsula. These alpine *Sieversia* species are very difficult to grow in lowland gardens.

The species of the subgenera *Sieversia* and *Eugeum* cross with ease, and some of the hybrids are moderately fertile (Gajewski, 1952). The hybrid between the

14-chromosome *G. montanum* and the 21-chromosome *G. rivale* is even 15 to 20 per cent fertile, and at meiosis has 14 paired and 7 single chromosomes, indicating that these species have 14 chromosomes in common. In the cross between the 21-chromosome *G. reptans* and the 21-chromosome *G. rivale,* 14 chromosomal pairs are also formed, but the other 14 chromosomes of the hybrid remain single. This behavior suggests that two sets of *rivale* chromosomes are homologous with two sets of 7 each from *reptans;* the third set, however, is different in the two species. Many F_1 seedlings of the hybrid *rivale* × *reptans* die early; others grow vigorously and blossom from spring to fall. The pollen is about 10 per cent fertile, but only 2 seeds were obtained from nearly 1000 flowers, and neither germinated.

The inheritance of the style shape of the cross *Geum montanum* × *G. rivale* is of considerable evolutionary interest because the parent species utilize two distinct systems of seed dispersal. The *montanum* parent has a persistent, straight, feathery seed tail about 30 mm. long. In contrast, in *rivale* the tail is ciliate, only 15 mm. long, and is looped at a distance of 9 to 10 mm. from the fruit, where eventually the tail end becomes detached, leaving a dry, hooked rostrum attached to the fruit. Botanically, the "seeds" are separate nuts on the floral receptacle, and the "seed tail" is the style, which ends in the stigma.

In the F_1 of *G. montanum* × *G. rivale* the seed tails are about 16 to 18 mm. long, but with respect to the loop there can be three different kinds of tail on the same F_1 plant, and even in the same flower. Some seed tails are straight as in the *montanum* parent and remain attached in their entirety. Other seeds have tails that are looped like the tails of the *rivale* parent; in these the stigmatal end becomes detached from the base through an abcission layer so located that the seed rostrum ends in a hook. Seeds of a third group have tails with a curvature where otherwise the loop would occur; the top of the seed tail dries and becomes detached, but the persisting rostrum does not become hook-tipped. The frequencies of these three kinds of seed appendage vary from plant to plant among the F_1.

In the F_1's of *G. montanum* crossed with *G. urbanum,* with *coccineum,* with *aleppicum,* or with *macrophyllum,* there is a similar variation in seed tail within each plant. When, however, *montanum* is crossed with *molle, hispidum, canadense,* or *silvaticum,* only straight seed tails are produced in F_1 progeny.

The cross *Geum montanum* × *G. rivale* was sufficiently fertile so that a second generation of 66 plants was obtained despite the difference in the number of chromosomes of the parental species. Because of the chromosomal differences the segregations cannot be used for a Mendelian analysis, but 56 of the 66 F_2 plants had the *rivale* type of style to a greater or lesser degree, 4 plants had the straight pinnate style as in *G. montanum,* and 6 had mixed types of styles as in the F_1. Among 46 plants resulting from backcrossing the F_1 to *G. rivale,* 43 had the *rivale* type of style, and only 3 were of the F_1 type. All 8 backcross individuals to *G. montanum* had fairly straight pinnate styles. These frequencies

suggest that the hybrid progeny may rather quickly revert to one or the other of the parental patterns with respect to the type of seed appendage.

The segregations in the *G. montanum* × *G. rivale* hybrid for seed tail concern a character that has been used taxonomically in separating genera. The heredity of this character controls two ecologically significant modes of seed dispersal. Anatomical studies indicated that even those hybrid seed tails that are straight pass through a slightly curved stage of development, whereas tails of seeds of nonhybrid *montanum* are always straight. Apparently a series of multiple genes controls the differences in seed appendage, and the expression in the F_1 varies with the stage of development.

The data suggest that *Geum* and *Sieversia* belong to one genus. The differences in seed appendage between the two determine whether the seeds will be scattered by wind or by furry and feathery animals. The *Sieversia* type in which a feathery straight style persists in its entirety appears to be the simpler arrangement. The *Eugeum* situation in which a loop and an abscission layer above the loop are formed seems to be the more specialized. In *Potentilla glandulosa* the style is short and undifferentiated; it is detached at the base, and the seeds are scattered by shaking of the inflorescence. The persistent dry calyx that surrounds the seed receptacle delays the scattering.

SUBSPECIFIC DIFFERENCES IN LAYIA INVOLVING CHARACTERS OF TRIBAL SIGNIFICANCE. An example of an ecotype's having become so highly differentiated from other members of the species in key morphological characters that its taxonomic placement even within the tribe was a matter of difficulty was found in *Layia glandulosa* (Clausen, Keck, and Hiesey, 1947*a*; Clausen, 1951). A rare endemic belonging to the Compositae was discovered by Mrs. Roxana Ferris and Dr. Ira L. Wiggins in a serpentine area in a semidesert in the inner Coast Range of central California. Because of its peculiar combination of floral characters, it would not fit taxonomically into any of the genera described in the Compositae, and was given the provisional name *Roxira serpentina.* Cytological and genetic evidence later demonstrated, however, that *Roxira* is merely a local edaphic subspecies of *Layia glandulosa* Hook. et Arn., a widespread species occurring in desert areas in California and adjacent western states.

Absence of ray florets and bracts enfolding the akenes on *Roxira* made its initial taxonomic placement difficult; in other characters it conformed with other members of the subtribe Madiinae and the genus *Layia.* It had 8 pairs of chromosomes; when it was intercrossed with the 8-chromosome but large-rayed *Layia glandulosa* the resulting F_1 hybrids proved to be fully fertile, and a complete segregation was observed in the F_2 ranging from rayless to fully rayed forms. In F_1 cultures, plants having 3 to 5 rays per head early in the flowering season later developed rayless heads. On the same plant, therefore, flower heads both with and without rays could be observed. An F_2 population of 1238 plants yielded 988 plants with rays and bracts and 250 that were rayless and bractless. Within the rayed group the number of rays per head varied between 1, 3, 5, and

8. In all these classes the length of rays also varied from very short to long. The over-all ratio between rayed and rayless plants was approximately 13:3 (theoretical distribution, 1005.8:232.2).

The two-gene 13:3 segregation may be explained by assuming that the development of ray florets is controlled by the interaction among positive and inhibitory genes. These assumptions can be expressed by assigning to the rayless *Roxira* the formula $r_1r_1I_2I_2R_2R_2$, and to *Layia glandulosa* the formula $R_1R_1i_2i_2R_2R_2$. Both parents accordingly are homozygous for a basic hypostatic gene, R_2, that controls development both of ray florets and of the bracts that envelop the ray akenes in the Madiinae. In this system, I_2 is an epistatic inhibitor of R_2, and R_1 an epistatic gene for ray florets and bracts, normally suppressing the effect of the inhibitor I_2. The F_1 would be $R_1r_1I_2i_2R_2R_2$, having ray florets because of the epistatic R_1, although toward the end of the season the single inhibitor I_2 is able to inhibit not only R_2 but also the heterozygous R_1r_1.

The rayed F_2's would be composed of 9 R_1I_1, 3 $R_1i_2i_2$, and 1 $r_1r_1i_2i_2R_2R_2$, whereas the 3 nonrayed plants would have the formula $r_1r_1I_2R_2R_2$. The observed ratio for the segregation, however, is much closer to 51 rayed plants to 13 rayless than to 13:3. The ratio 51:13 would require the F_1 to be heterozygous also for R_2, so that it would have the formula $R_1r_1I_2i_2R_2r_2R_3R_3$. On the latter assumption the expectation would be 250 nonrayed plants among the 1238 F_2 individuals, the number actually observed. In the absence of F_3's it is not possible to distinguish between these two possibilities. The F_2 data nevertheless strongly indicate that the key character delimiting the two entities in this case is controlled by two or three pairs of genes of oppositional effect. Other gene systems control the number of rays per head and the length of the rays.

Roxira differs also from *Layia glandulosa* in having short, stubby pappus as compared with long, tapering pappus in *glandulosa*. In the F_2 there were 1212 plants having long to medium pappus, and only 25 plants with pappus as short as that in *Roxira*. This segregation approaches a 63:1 ratio (theoretically 1218.7:19.3) and suggests that with regard to this character *Roxira* is recessive for three pairs of genes.

The parental character combinations are strongly favored through correlations, for 15 of the 25 F_2 plants having short pappus occurred among the 250 nonrayed plants, and the other 11 were distributed among F_2 plants having short to medium rays, and among those having less than 8 rays per head (table 1, Clausen, Keck, and Hiesey, 1947*a*). A correlation exists, therefore, between short pappus and short rays or none, all characters introduced by the rayless *Roxira*.

Evolutionarily, it is of interest to speculate on how these edaphically distinct entities of *Layia glandulosa* became so different. Ecologically, sandy and serpentine soils are so distinct that they often are occupied by distinct species of the same genus. Walker (1954) emphasized the very low degree of available calcium in serpentine soils as compared even with sandstone. Kruckeberg (1951, 1954) showed that species such as *Gilia capitata* Dougl. of the Polemoniaceae,

Salvia columbariae Benth. of the Labiatae, and *Achillea borealis* Bong. of the Compositae all grow on both serpentine and nonserpentine soils, but that they have evolved edaphically distinct ecotypes. In these three species, ecotypes native to nonserpentine soils are barely able to survive when planted in serpentine. In contrast, forms native to serpentine soil, although growing better on serpentine soil, readily tolerate nonserpentine.

When *Roxira serpentina* was transplanted from its serpentine habitat at New Idria to the nonserpentine soil of the experiment garden at Stanford, it flourished moderately and increased in height from 5–15 cm. in its native site to 15–25 cm. at Stanford, where it nevertheless remained smaller than most strains of *Layia glandulosa.* Since there is evidence of genetic linkage for other characters in the complex, there is a possibility that the recessive r_1 gene is linked with ability to tolerate serpentine. Natural selection working with a mixture of biotypes would in such a case tend to select the nonrayed form on serpentine soil, and the rayed *Layia glandulosa* on nonserpentine soil.

In the Madiinae in general, species having large, conspicuous rays are self-incompatible and require cross pollination, whereas those with small, inconspicuous rays are self-compatible. *Roxira,* however, remains self-incompatible like other members of *Layia glandulosa* even though it has lost its rays.

Inheritance in spatially isolated subspecies of Hemizonia angustifolia. In some species composed of more than one subspecies the isolation between subspecies is spatial rather than ecological. The coast tarweed of California, *Hemizonia angustifolia* DC., is an example. It is separated into two morphologically distinct population complexes by a mountain barrier, with no evidence of ecological distinctness between the subspecies that occur in the two areas (Clausen, Keck, and Hiesey, 1947*a*; Clausen, 1951).

The coast tarweed of the Madiinae occurs along the narrow coastal strip of the foreland between the outer Coast Range and the Pacific Ocean over a distance of nearly 600 km. from north to south. South of Monterey Bay the coastal plain is interrupted by the Santa Lucia Mountains, which rise directly from the ocean for a distance of 65 km. The northern subspecies, *angustifolia,* occupies a strip 450 km. long north of this barrier, and does not change perceptibly over that distance. The southern subspecies, *macrocephala* (Nutt.) Keck, occurs south of the barrier and inhabits a strip 60 to 70 km. long. The southern subspecies has more erect growth than the northern, and larger and more congested heads. In the uniform garden at Stanford, however, the time of flowering was the same for populations of both subspecies originating from the northernmost to the southernmost part of their respective ranges.

Both subspecies have 10 pairs of chromosomes and are fully interfertile. An F_2 population of 1300 individuals was grown, of which 1152 were tabulated. All three characters distinguishing the parents segregated by small steps, but the parental equivalents of each character were recovered. The segregation was by multiple genes, the minimum number governing paired character contrasts

being approximately four or five. The F_1 was intermediate, and the F_2 segregation was symmetrical if a small group of constitutionally weak F_2 plants was disregarded. These facts indicate that the multiple genes were of the cumulative type. The difference between the two subspecies is, therefore, of a kind that could have arisen simply through isolation and genetic drift.

This example fits the tenets of orthodox population genetics because the gene differences apparently are of the kind assumed in deriving mathematical formulas. Both subspecies are distinctly coastal in their ecology, and the morphological separation in this instance was not accompanied by ecological differentiation.

INTERCONTINENTAL SUBSPECIFIC DIFFERENTIATION IN PLATANUS. The planes or sycamores of the genus *Platanus* belong to one of the geologically oldest genera of the angiosperms. A fairly uninterrupted record of this genus exists from mid-Cretaceous to the present time. Possibly starting in North America some eighty million years ago, the genus accompanied the Magnolias and the Liquidambars in their spread around the world, and many fossil species of *Platanus* have been recognized. In the late Cretaceous the planes had already made their appearance at Disko, 4° north of the Arctic Circle in western Greenland, as is evidenced by fossil deposits.

Today the family Platanaceae consists only of the genus *Platanus,* having three or four named species that possibly do not even have genetic barriers. All these species are native to middle northern latitudes in fairly warm climates. Except in the Himalaya, where the planes ascend to more than 2000 m. altitude, and in eastern North America, the present-day species of *Platanus* are limited to stream banks of the New and Old World.

The oriental plane, *Platanus orientalis* L., is native to the eastern Mediterranean area including Asia Minor and Syria, but extends eastward to the Himalaya. The tree was cultivated in Roman times, and spread with Roman civilization, but the strains used were tender and unable to tolerate the colder winters as that civilization moved northward. After the discovery of North America the eastern North American species, *P. occidentalis* L., from a much colder winter climate, was introduced to European gardens. Apparently the two species *P. orientalis* and *P. occidentalis* hybridized spontaneously in the Oxford Botanical Garden around 1670 (Henry and Flood, 1919). The hybrid, *P. acerifolia* (Ait.) Willd., the London plane, combines morphological characters of the two parents, tolerates cold winters better than the oriental plane, is more vigorous than the parents, and appears to be fully fertile. The progeny are variable but vigorous, and are being grown at many latitudes around the world in gardens and along city streets and roadsides. The tree is sometimes propagated by rooted cuttings to ensure uniformity in plantings.

Both *Platanus acerifolia* and *P. occidentalis* have 21 pairs of chromosomes. Winge (1917) and Sax (1933) found the pairing to be exceedingly regular between the Mediterranean and the American species. Although counts on chro-

mosomes of properly identified *P. orientalis* have not yet been reported, it may be inferred that this species, like *P. occidentalis,* whose number was established by Sax, also must have 21 pairs; the perfect pairing in the hybrid leaves little doubt about the chromosome number in the oriental plane.

The third species of the genus, *P. racemosa* Nutt. (including *P. wrightii* Wats.), is a stream-bank species in southwestern United States and northern Mexico. Morphologically and ecologically it is much closer to *P. orientalis* of the Old World from a similar climate than it is to its geographical neighbor, *P. occidentalis* of the eastern United States.

The chromosome number $n=21$ strongly suggests that our present-day planes are very old polyploids, possibly hexaploids. The American and European species must have attained this chromosome number before they separated, millions of years ago. It is an arresting thought that the chromosomal apparatus of the North American and the European species has not undergone any major change during this immense span of time, and that the chromosomes have preserved their full homology. It appears that under certain conditions the structure of chromosomes may be exceedingly stable.

The eastern North American and the oriental planes are kinds of living fossils. Biologically, they are still conspecific. Morphologically and ecologically, however, they are contrasting races or subspecies. The success of the intercontinental hybrids adds emphasis to the observation that interracial hybrids are often highly tolerant to a great range of climates.

GENETICS OF ECOLOGICAL RACES IN THE ANIMAL KINGDOM

The heredities that control ecological races of animal species are generally less well known than those of ecological races of plants. In certain groups of animals, however, it is now possible to ascertain some of the genetic patterns that are related to adjustments to environment. Three examples, *Drosophila pseudoobscura, Rana pipiens,* and *Lymantria dispar,* will be discussed in some detail in the following pages.

Besides these three species, some information on the heredity of ecological races is available for altitudinal and edaphic races of the deer mouse, *Peromyscus maniculatus,* and relatives (Dice, 1933*a,* 1933*b,* 1940, 1942); the fresh- to salt-water races of the stickleback fish, *Gasterosteus aculeatus* (Heuts, 1946, 1947*a,* 1947*b,* 1949*a,* 1949*b*); and regional and edaphic races and species of the alfalfa butterfly, *Colias* (Hovanitz, 1945*a,* 1945*b,* 1949). These experimental studies show that the adaptive differences among the races are hereditarily controlled, and that sometimes the control is implemented by differences in physiology.

Altitudinal and seasonal variation in Drosophila. The fruit flies of the genus *Drosophila* have been favorite subjects of genetic investigations. The cosmopolitan garbage species of the genus, such as *Drosophila melanogaster,* have obscure ecological relations and are therefore of little interest for ecological

genetics. The western North American fruit fly, *Drosophila pseudoobscura,* on the other hand, has natural populations in the forests and mountains of the western United States and Canada. Dobzhansky and collaborators have studied the variability of this wild fruit fly in relation to environments across a part of the same central California transect that furnishes habitats for ecological races of *Potentilla glandulosa.*

The genetic structure of *Drosophila pseudoobscura* differs markedly from that of *Potentilla glandulosa,* for in the fruit fly genetic diversification is characterized by numerous chromosomal rearrangements of gene sequences throughout the 5 pairs of chromosomes of this species. The rearrangements are mainly inversions which prevent crossing-over within the inverted segment. The inversions can be identified and readily studied in the giant chromosomes of the salivary glands.

Concentrating on the study of chromosome III of *Drosophila pseudoobscura,* Dobzhansky (1948, 1949) found that the populations along the transplant station transect of the Sierra Nevada in California were composed of flies having various chromosomal arrangements. The three most common are known as Standard, Arrowhead, and Chiricahua. The frequencies of these chromosomal arrangements in a population vary with the season and with altitude. An individual fruit fly, possessing one pair of third chromosomes, may have as many as two of these three arrangements, or may have combinations with other, rarer inversion types.

At localities across the Sierra Nevada where the populations were sufficiently sampled, the Standard arrangement was found to increase in relative frequency as the season advanced from cool spring to warm summer. In contrast, the Arrowhead arrangement was found to be most frequent in spring and less frequent as the season advanced to summer. Chiricahua was found to remain relatively constant in frequency throughout the season. A fourth and less common inversion, Timberline, has its greatest frequency at both ends of the season, during early spring and autumn.

Besides the seasonal shifts in frequencies of arrangement, there is an altitudinal gradient in the relative frequencies of the Standard and Arrowhead arrangements ranging from 250 m. in altitude on the lower western slopes of the Sierra Nevada to 3000 m. at Timberline. Between 250 and 1000 m., Standard was found to be the most frequent arrangement, and Arrowhead and Chiricahua less frequent. Between about 1300 and 2000 m. the Standard and Arrowhead arrangements exchanged position in relative frequency: here Arrowhead had become the generally most frequent, Standard the next, and Chiricahua remained the least frequent. From about 2500 to 3000 m. altitude, however, Standard became the least frequent and Chiricahua number 2, Arrowhead remaining number 1 in frequency. The Chiricahua arrangement showed only minor changes in relative frequencies along the transect. At altitudes between 250 and 2000 m. its relative frequency was 16.2 per cent of the chromosomes

tested within the population, and in five samples from altitudes between 2600 and 3000 m. it averaged 23.1 per cent, possibly a significant increase.

Both seasonally and altitudinally, therefore, the Standard arrangement increases in frequency with rise of the temperature, whereas Arrowhead decreases, and Chiricahua shows minor changes in the same direction as Arrowhead.

These effects suggest that *Drosophila pseudoobscura* meets the requirements of the environment in a very different manner from that of perennial plants, which must survive through both favorable and unfavorable seasons. *Drosophila* can produce a new generation every two or three weeks and may therefore utilize a genetic mechanism for quickly changing the composition of the local population according to the season. Through the same mechanism of selection, the composition of the various populations changes with altitude.

The adjustment of *Drosophila pseudoobscura* to changes in the environment occurs through shifts in the frequencies of individuals having particular inversion segments of chromosome III. The inverted segments of this chromosome become balancing elements that adjust the fly to its environment, and it must be assumed that the inverted sectors contain blocks of genes having distinct physiological effects on the development of the fly. Because gene interchange is eliminated throughout the inverted sector, the series of genes carried in the sector function as a supergene.

Not only do populations of *Drosophila pseudoobscura* change the relative frequencies of the various chromosome III arrangements as one moves from west to east over the transect of the Sierra Nevada, but the shift continues eastward throughout the southern part of the Great Basin over northern Arizona and New Mexico to the southern Great Plains in central Texas (Dobzhansky, 1947). Over this arid transect the Standard arrangement decreases sharply in frequency, and Arrowhead increases equally sharply with increasing aridity, suggesting that moisture relations may be important in determining the balance between the two arrangements. East of the Continental Divide the Pikes Peak chromosomal arrangement begins to appear, and in Texas it becomes the most common one.

At any one location many individuals are heterozygous for the arrangements of chromosome III. Heterozygotes of, for example, Standard with Arrowhead, or with Chiricahua, have a higher frequency in the populations than would be expected on the basis of the observed frequencies of the corresponding homozygotes; the inversion heterozygotes, therefore, appear to have greater viability. This increased viability of inversion heterozygotes in *Drosophila* parallels the increased vigor and viability in interecotypic hybrids in plants.

In perennial plants, morphological markers often characterize distinct ecotypes. The markers may not themselves facilitate ecological adjustment of the race to the environment, but may be linked with genes that control physiological characters of importance in determining adjustment to the environment. Likewise, in *Drosophila pseudoobscura* it is clearly not the particular chromosomal arrangement that induces fitness to a certain environment, but rather the genes

that are grouped in the inverted segment and happen to control processes of importance in adjusting fly populations to seasons and altitudes.

Dobzhansky (1949) tested the relative adaptedness of various chromosomal arrangements in competition experiments in artificial populations kept in small cages under controlled temperatures. The density of individuals in these cages greatly exceeded that in the wild. The populations were started with a known number of heterozygotes and of the corresponding homozygotes. It was found that, at 25° C., in successive generations over a period of months all three heterozygotic combinations of the three arrangements increased in frequency faster than the homozygotes.

When the experiments were conducted at 16° C. instead of at 25° C., however (Dobzhansky, 1949, pp. 214–215), an interesting discovery was made which has received little attention. At this lower temperature, no shift took place in the original frequencies of the heterozygotes and homozygotes month after month. The competitive value of the inversion heterozygote at 16° C., therefore, roughly equals the competitive values of the corresponding parental homozygotes, whereas at 25° C. the competitive value of the Chiricahua-Arrowhead heterozygote is about twice as high as that of the homozygotes.

In climatic terms, the difference between 16° and 25° C. corresponds approximately to the difference between summer temperatures in central Alaska and New York. Distinct plant biotypes would typically show a great shift in degree of tolerance over such a range. It is of considerable interest that *Drosophila* may do the same. In an inversion heterozygote the inverted segment represents a large block of genes. The expression of this complex of genes is obviously influenced by temperature.

The adaptive or competitive value of the inversion heterozygotes was reduced, or even lost, if the two chromosomes of the heterozygote originated from considerably different latitudes (Dobzhansky, 1950). Three sets of Standard, Arrowhead, and Chiricahua arrangements were used that had originated, respectively, at Mather at about 38° N.; at Piñon Flat, in the San Jacinto Mountains in southern California at 35.5° N.; and at Chihuahua, Mexico, at about 28° N. In these experiments it was found, as an example, that the inversion heterozygote composed of the Arrowhead arrangement from Mather and the Chiricahua arrangement from Piñon Flat was inferior in viability to the homozygotic Mather Arrowhead arrangement, but that, in turn, the heterozygote was much superior to the homozygotic Chiricahua arrangement from Piñon Flat. The viability of these interlatitudinal inversion heterozygotes was therefore intermediate between those of the corresponding homozygotes.

In testing the Piñon Flat, California, arrangements with those from Chihuahua, Mexico, it was found that the inversion heterozygote composed of the Arrowhead arrangement from Piñon Flat combined with the Chiricahua arrangement from Chihuahua was even inferior to both the parental homozygotes. In this particular cross the ecological advantage of the inversion heterozygote was

completely lost, although it is possible that at a higher temperature than 25° the heterozygote might have proved to be the most viable.

It is possibly an evolutionary accident that the inversion heterozygotes of chromosomes from different latitudes happened to have a lower competitive value than the inversion heterozygotes of chromosomes from the same latitude. It might just as well have happened that they had increased in adaptiveness, or that there had been no difference. It is also possible that this particular response is a function of the chance temperature under which the chromosome arrangement was tested.

The observed greater frequency of the inversion heterozygotes as compared with homozygotes in wild populations may tend to preserve the particular arrangements from destruction through elimination. As the temperature drops below the average of 25°, however, some of the advantages of the heterozygotes may be lost, although samplings indicate that the balance in the population system is such that all arrangements persist, though sometimes at low frequency.

The major facts that emerge from these significant and well documented investigations are that the relative frequencies of the inversion arrangements change with the season and the altitude, and that there also is an adjustment to latitude. The shifts in population composition occur constantly during the season, continuously adjusting the species to its environment. The ecotypic adjustment to the environment is by chromosomal arrangements, and it is dynamic and flexible.

GENETIC-PHYSIOLOGIC INCOMPATIBILITY BETWEEN REGIONAL ECOLOGIC RACES OF RANA PIPIENS. The North American leopard frog or meadow frog, *Rana pipiens* Schreb. (including *R. brachycephala* Cope and *R. sphenocephala* Cope), has a wide geographical range. It occurs from 9° N. in Costa Rica northward to 60° N. in Canada. Altitudinally it occupies habitats from near sea level to 3000 m. (Moore, 1950; Ruibal, 1955), and longitudinally its area extends from the Atlantic coast to the Sierra Nevada and Cascade Mountains (Moore, 1949*b*). Within this territory the species shows considerable morphological variation (Moore, 1944).

Ecologically more significant is the fact that the races of the leopard frog differ in their ranges of temperature tolerance. In experiments under controlled temperatures Moore (1939, 1942; 1949*a*, fig. 8) found that in populations ranging from 40° N. in New Jersey to 46° N. near Montreal, Canada, the incubating eggs will tolerate a range of temperatures from about 6° C. to about 28° C. Below or above these temperatures the embryos develop abnormally or die.

The embryos of a series of southern populations, ranging from latitude 32° N. at Monahans, Texas, to 27° N. at Englewood, Florida, succeeded over a range of somewhat higher temperatures. The embryos from these populations are unable to tolerate temperatures below 10° C., but will grow at temperatures up to 32° C., and the Englewood population will live up to 35° C. A population from Chalmette, Louisiana, at 30° N. combined the tolerance for low tempera-

tures of the northern populations with the tolerance for higher temperatures of the southern populations.

The embryos of a population from near Axtla, in the state of San Luis Potosí, Mexico, at 22° N., degenerated at the low temperature of 10° C. and were highly retarded at 12° C., temperatures at which the population from Alburg, Vermont, at 45° N. developed normally.

On the whole, at the lower temperatures the southern populations developed more slowly than those from higher latitudes, whereas at higher temperatures the southern populations overtook the northern in normal development. It is therefore clear that physiologically and developmentally populations from north of latitude 40° are distinct from those native to latitude 32° and southward. Four populations from New Jersey, Vermont, Montreal, and Wisconsin followed essentially the same developmental curve over their entire tolerance range (Moore, 1949*a*). Compared with the curve of the northern racial complex, the populations from Texas, Louisiana, Florida, and Mexico all develop more slowly at the lower half of the temperature range (below 18° C.), but at higher temperatures they develop the faster. The temperatures at which the southern populations overtake the northern differ from race to race. The difference in responses between the northern and southern population complexes of meadow frogs appears to be comparable to that of latitudinal ecotypes of plants from equally dissimilar environments.

Rana pipiens has not only latitudinal but also altitudinal races. Frogs were collected at three contrasting altitudes in southern Mexico (Ruibal, 1955), namely, at San Diego, in the state of Puebla, at 263 m. altitude; at Rio Tula, Hidalgo, at 1600 m.; and at Lagunas de Zempoala, Morelos, at 3000 m. altitude. This series of altitudes is somewhat comparable to the Stanford-Mather-Timberline series except that the Mexican series is in the vicinity of the 20th parallel of latitude instead of the 38th. When the development of the embryos of frogs from the Mexican altitudinal series was tested at a series of controlled temperatures, it was found that the developmental curves of the races from the three altitudes were parallel within the temperature range tested, namely, between 13° and 28° C. The low-altitude race developed fastest at all temperatures; the high-altitude race was the slowest; the mid-altitude race, intermediate. The parallelism of the curves of the altitudinal series contrasts with the crossing of the curves of the high- and the low-latitude races.

Moore (1946*a*, 1947, 1950) and Ruibal (1955) produced many hybrids between individuals of the populations of *Rana pipiens* from various climates. These hybrid populations were not developed beyond F_1. It was attempted to raise them to the stage of metamorphosis, the adult frog stage, or at least to the tadpole stage. Many hybrids succumbed earlier, however.

In intraracial crossings between the populations of the northern race from latitude 40° to 45°, such as Vermont crossed with Wisconsin and New Jersey, the F_1 individuals developed normally and were readily raised to metamorphosis (Moore, 1946*a*). The embryos were developed at temperatures of 19°, 22°,

and 24° C., well within the optimum of all the races. Even the crossing between the Vermont population and a mid-altitude population from near Boulder, Colorado, at 2700 m. altitude and 40° N., resulted in a perfectly harmonious F_1 combination (Moore, 1950). Likewise, in crossings within the southern race, such as Ocala or Englewood, Florida, with Louisiana, the F_1's developed normally and completed their metamorphosis.

When members of the northern race were crossed with members of the southern, however, the F_1's had developmental difficulties. The early development of the embryo was usually normal, but in later stages these interracial hybrids were distinctly retarded in development, and abnormalities such as lack of olfactory pits, lack of mouth, small mouth, or much enlarged or diminished heads appeared. In some cases there was defective gill circulation. Judging from these abnormalities, it appears that the genes that control the developmental processes in the parental races are so different that when combined in the F_1 they are thrown out of balance.

In interracial crossings between the Vermont race of *Rana pipiens* from 45° N. and races from Mexico at 26° N. (Monterrey) and 22° N. (Axtla), the abnormalities in the F_1's were even more startling. The hybrid embryos were highly defective, and most animals died within 2 weeks. The best survival was in the hybrid Vermont × Monterrey, in which 10 per cent of the embryos survived for 130 days.

In crossings between the local races from Mexico, Ruibal (1955) found that the F_1 progeny between two low-altitude populations from San Diego and Villa Juarez (both in the state of Puebla) were normal. So were the F_1's between the two high-altitude populations from Zempoala, Morelos, at 3000 m., and El Chico, Hidalgo, at 2900 m. When the lowland San Diego population was crossed with the high-altitude Zempoala, however, some developmental disturbances were noted in the F_1's, especially in rate of development. Some tadpoles were raised from the cross San Diego × Zempoala that metamorphosed normally, whereas other F_1 individuals died early. The mid-altitude population from Rio Tula, Hidalgo, at 1600 m. altitude, when crossed with either the high-altitude Zempoala or the low-altitude San Diego, produced normal F_1's, although there was some modification in the rates of their development. The unbalance in hybrids between altitudinally distinct races of *Rana pipiens* is therefore relatively slight.

When the Vermont race was crossed with the three altitudinal Mexican races, all the F_1's showed retardation, disturbances, and high mortality. The highest mortality, 43 to 100 per cent, occurred in hybrids between Vermont and the lowland San Diego race, and the lowest mortality, 6 to 31 per cent, in the F_1's of Vermont crossed with high-altitude Zempoala. These data found by Ruibal are consistent with Moore's previous findings.

Exceptions may be found to the rule that races of *Rana pipiens* from latitudinally highly distinct zones are incompatible. Moore (1950) crossed a race of the leopard frog from near the southern limit of the species at Moravia,

Costa Rica, at about 10° N. and at 1200 m. altitude, with females from Vermont originating at 45° N. The F_1 hybrids showed slight disturbances in the early stages of their development, but later recovered, hatched normally, and developed into healthy tadpoles.

Evidently, in their adjustment to climates of contrasting latitudes, the leopard frogs have evolved ecologically distinct races that are usually genetically so specialized that they are unable to produce healthy and normal hybrids with each other. In this kind of differentiation, the ecological races of *Rana pipiens* behave like distinct species. Apparently, however, the race from Costa Rica at the extreme south of the distribution of the species is genetically highly tolerant. Located at the outskirts of the area of the species, this particular race has apparently not participated in the genetic-physiologic specialization characteristic of the ecological races of the northern and the southern United States and of Mexico.

Further evidence that the genetic-physiologic barriers that separate the northern and the southern races of *Rana pipiens* do not represent changes of great phylogenetic significance is found in the fact that the pickerel frog, *Rana palustris* Le Conte, is genetically compatible with populations of *Rana pipiens* from all latitudes. Moore (1946*b*) crossed a fairly high-latitude form of *Rana palustris* from Massachusetts with *Rana pipiens* from Wisconsin, Vermont, and New Jersey, and likewise with populations of the southern race from Oklahoma, Texas, Louisiana, and Ocala and Englewood, Florida. In two of these combinations minor retardations or accelerations were noticed in the development of F_1 embryos, but these and all other hybrids were nevertheless raised to tadpoles and to metamorphosis.

The area of the pickerel frog overlaps that of the leopard frog, and the curves for their temperature responses are closely similar (Moore, 1942, figs. 2, 3), but the two groups differ in their ecologic preferences and spawning periods. Since data from F_2 populations are lacking, it is not possible to determine whether these two taxonomic entities are genetically separated, or whether they are but edaphic subspecies. The success of the F_1 hybrids suggests, however, that the strong genetic barriers observed between the northern and the southern races of *Rana pipiens* are of fairly recent origin, since both these races can be successfully linked through *Rana palustris,* which apparently has a more tolerant genetic structure.

Other species of the genus *Rana* are genetically well separated, as is indicated by many attempted crosses by Moore (1949*b*). Several of the species are genetically so distinct that no cleavage occurs in the fertilized F_1 eggs (Moore, 1949*b,* p. 332). Other F_1 combinations fail at the beginning of gastrulation, some fail at the neurula and tailbud stages, and a few F_1's develop normally to adults. In this animal genus, therefore, is observed a gradation with regard to the genetic separation of species similar to that existing within many plant genera.

In the *Rana pipiens* complex the development of strong genetic barriers between certain latitudinal ecotypes indicates the early stages of differentiation

into genetic species. The more tolerant common denominators, such as the Costa Rica race of *Rana pipiens* and the closely related *Rana palustris,* which form compatible combinations with ecological races of *R. pipiens* that are noncompatible among themselves underscore the close relationships among the leopard frogs.

HEREDITY OF ADAPTIVE CHARACTERS IN ECOLOGIC RACES OF LYMANTRIA. Possibly the most extensive investigation ever undertaken on the genetic structure of geographic-ecologic races of a species was that on *Lymantria* by Goldschmidt (1924–1933, I–VII; 1932*d,* 1934, 1940). The gypsy moth, *Lymantria dispar* L., is a pest on deciduous trees in the temperate zone of Eurasia. In its composition of races, its genetic structure, and its adjustment to the environment, the gypsy moth shows a great deal of similarity to plant species of similar distribution.

The gypsy moth belongs to the family Lymantriidae. The majority of genera and species of this family are natives of India, Malaysia, and Africa, but two species are members of the fauna of the northern temperate zone. The species under discussion, *Lymantria dispar,* occurs between latitudes 30° and 60° N.; the other species of temperate latitudes is the dangerous pest *L. monacha* L., the nun moth. In some of the genera of the Lymantriidae the adult females are almost wingless.

Lymantria dispar has $n=31$ pairs of chromosomes, suggesting a fairly complex genetic structure. Its larvae feed on the young spring foliage of deciduous trees, such as various species of oak, fruit trees, beech, and willow, and are therefore not highly selective with regard to food. Throughout its distribution this species apparently has latitudinal and altitudinal ecological races similar to those of *Rana pipiens* and of many plant species; the concentration of races of *Lymantria* is especially great in topographically and climatically varied Japan. *Lymantria dispar* has been introduced to North Africa and to Massachusetts in North America.

In spring, after the food plants have come into leaf, the larvae of the gypsy moth emerge from their eggs and begin to feed on the tender spring foliage. After four or five stages of molting, depending upon the race, they pass into the pupal stage, which lasts about 2 weeks. The adult moth emerges during July or August. The females are sedentary and remain on the bark of the tree where they have been hatched, waiting for the males, which swarm about. After mating, the female deposits a batch of several hundred eggs, pasting them to trees, roofs, or stones, and then covering them with a feltlike layer of hairs rubbed from her abdomen. Without ever having taken food, the adult female dies after having performed this function.

After about 6 weeks tiny young larvae develop within the eggs; they hibernate, and do not emerge until the next spring, during late April or May. The time of emergence of the larva from the egg is closely correlated with the leafing of food plants. Since it would be disastrous for the new generation of caterpillars to emerge before the leaves appeared, natural selection must have taken

place, resulting in an adjustment of the time of emergence of the caterpillars and the host vegetation.

One of the most important ecological differences among races of the gypsy moths from various climates is the time required for development from egg to caterpillar stage under various temperatures. When the eggs are wintered outdoors, the larvae of particular races emerge with remarkable precision in timing. Under controlled laboratory conditions the eggs can be hatched by being placed in incubators at various temperatures and at various seasons (Goldschmidt, 1932*c*). The gypsy moth is therefore well suited to experimental work on ecological races. In the laboratory, genetic variations not evident under natural conditions can be discovered among individuals of a single population.

The hatching period depends on the season at which incubation is initiated, the temperature at which the eggs are incubated, and the genetic characteristics of the race. In a typical experiment, batches of eggs native to different geographic regions were placed in incubators at constant temperatures of 11° and 21.5° C. on January 1, February 1, and March 1. A smaller number of populations and races were incubated at temperatures of 8°, 16°, 23°, and 25° C., starting at the same three initial dates as above.

At 11° C. and starting incubation on January 1, the first larvae may emerge from the eggs 23 to 84 days after the beginning of the experiment, depending upon the geographic origin of the race. The spread of time between the emergence of the first and last larvae under these conditions may range between 8 and 62 days.

When incubation is started at one of the later dates, the corresponding elapsed time is shortened. When incubation was started on March 1 and the temperature kept at 11° C., the time required for emergence of the first caterpillar varied between 24 days for the fastest responding population and 40 days for the slowest. The spread in days between the earliest and the latest emerging caterpillar of a single progeny under these conditions may range from 6 days for the most uniform to 26 days for the most variable.

The periods required for emergence of divergent races are also telescoped at higher temperatures. From eggs incubated at 21.5° C. the earliest caterpillars started hatching 15 days later, and the slowest after 30 days. The period required for all the caterpillars of a progeny to emerge under these conditions was also much shortened, there being a spread of 4 days for the most uniform, and 28 days for the most variable. At 21.5° C. and beginning at March 1, the earliest progeny began emerging after 9 days, and the latest after 20 days. In one series of experiments the range of variation within progenies was 4 days for the least variable, and 12 days for the most variable.

In other experiments (Goldschmidt, 1932*c*) eggs were kept out-of-doors near Berlin, Germany, until April 28, when they were placed at 25° C. The earliest progeny started hatching the following day, and most individuals within a progeny completed hatching within a single day, although in rare cases the range would extend over 2 days. Within 1 week, April 29 to May 5, all progenies

had hatched except two from Manchuria; one of these started on May 9; in the other, from Dairen, one batch of eggs hatched on May 14, and another on May 31. In the experiments using earlier starting dates for incubation and lower temperatures, the Manchurian race was always the last to hatch and had the greatest range of variability in hatching time.

In control experiments, the eggs of various races and progenies were placed out-of-doors at Berlin all winter without laboratory incubation (Goldschmidt, 1932*c*, pp. 743–746). During one particular year, 1931, spring was late and the earliest races did not start to hatch until May 9; before May 14, however, all except the Manchurian race had emerged. Under this natural condition all eggs of progenies from the same habitat hatched within a single day. In another experiment outdoors in 1929 that included the extreme races, except Manchuria, together with intermediates, hatching of all races was completed within the range of 6 days, between May 12 and May 18, 3 or 4 days later than in 1931. These observations indicate that under natural conditions moderate modifications occur from year to year that make hatching time coincide with the leafing of food plants.

The physiological control of hatching is so well balanced that under controlled temperatures the caterpillars of natural populations and races emerge in the same general order in experiments employing different temperatures and starting dates. Although various temperatures do not seem to change the order of hatching, they do affect the length of the period within which the caterpillars of given races emerge. There are a few exceptions to this generalization, however. The forms from Korea, which in all the controlled incubation experiments were among the earliest, were among the later forms in an outdoor experiment conducted in 1932.

The fastest-emerging race of the gypsy moth (Goldschmidt, 1932*c*, p. 743) was represented by the Bukhara and Samarkand progenies from Turkestan. At an incubation temperature of 11° C. beginning February 1, the mean incubation period for these two progenies was 33.3 days. The moths from this region belong to a climate having a very brief vegetation period in spring wedged between a cold winter and a hot and dry summer, and plants in this area emerge rapidly during spring. Another race from the Brandenburg plains, Berlin, Germany, having a cold winter and a hot, fairly dry summer, was almost as fast.

Consistently slowly developing forms included those from the Mediterranean region such as Sardinia (mean hatching period from February 1 at 11° C., 56 days), Castel Toblino (58.1 days), and Portici, near Naples (62.9 days). Fast-emerging races would be at a disadvantage in a region like the Mediterranean, because they would emerge during mild winter days when the leaves of their food plants are still leathery and indigestible.

Even slower in development than the Mediterranean is the Manchurian race as represented by progenies from Sanjuriko and Dairen. Under the same conditions as the above, the Sanjuriko progeny had a mean incubation period of 84 days, but only a few caterpillars emerged under these forced conditions; the

Dairen form was lost early in the experiments for the same reason. The lateness of the Manchurian race, native to a highly continental climate with a long, severe winter, is obviously of a different nature from the lateness of the Italian race from a Mediterranean climate with a mild winter.

Throughout Japan, from north to south, races are found having incubation periods intermediate between the extremes just discussed. Characteristic durations of incubation period were found among the progenies from within each of the regions, and the hatching time of the caterpillars under natural conditions in their native area was found to correspond to the period of leafing of the food plants in the region.

Goldschmidt (1932*c*, p. 713; 1934, pp. 129–132) found that a number of conditions must be fulfilled before hatching occurs. Chilling has a beneficial effect in inducing a more uniform hatching. Eggs not previously exposed to chilling sometimes do not hatch, and a higher temperature is required to induce emergence.

Hatching occurs also only within certain ranges of temperature. The caterpillars do not emerge if the temperature remains below a minimum of 4° to 6° C. The most favorable temperatures for hatching are between 10° and 20° C.; above 30° C. no emergence occurs. In early winter a temperature of 26° C. is almost lethal, whereas in spring hatching occurs freely at that temperature.

The most conspicuous requirement for the hatching process is that eggs arrive at the stage "readiness to hatch." A time element is included in this requirement. It does not suffice that the eggs are simply chilled, or that they are kept at the proper temperature for hatching, for they did not hatch properly in the January 1, February 1, or March 1 experiments. When the processes leading to the stage "readiness for hatching" have been completed by late April or early May, however, the caterpillars emerge promptly at the proper temperatures.

Finally, there are genetic factors that govern racial differences with respect to requirements for chilling, differences in minimum, optimum, and maximum temperatures, and differences in the time required to attain readiness to hatch. It is evident that genetic, physiologic, and environmental factors all interact in the hatching process.

There is a striking similarity in the kind of processes that are needed for the hatching of *Lymantria* eggs and the kind of processes that determine the flowering of plants such as the grasses *Lolium* and milo *Sorghum* discussed previously (pp. 224–228 and 228–232). The plants need to arrive at a time-related "readiness to flower," and *Lymantria* requires a similar "readiness to hatch." In both *Lolium* and *Lymantria,* chilling apparently speeds up some of the processes, whereas in the tropical grass *Sorghum* chilling is not required and is rather deleterious. Certain threshold temperatures are of significance in all three organisms, and the two grasses also have thresholds for day lengths that activate certain genes.

The data presented by Goldschmidt suggest that the interactions are strongly buffered under the conditions to which the race is native. When the organism

is reared under laboratory conditions that are quite different from those in the wild, an inherent genetic variability is expressed within each race that normally does not come to expression. This display of latent variability in *Lymantria* parallels that in *Lolium* and *Sorghum*.

An extensive genetic analysis of the inheritance of the length of incubation period (length of diapause) was conducted by crossing many contrasting races of *Lymantria dispar*, and by carrying the genetic analysis to the F_2 (Goldschmidt, 1932*c*, 1933*b*). Like ecological races of plants, and in contrast to many of the races of the leopard frog, ecological races of *Lymantria* can be freely intercrossed. Their F_1 hybrids are fully fertile, and huge F_2 progenies can be reared from them. Some of Goldschmidt's F_2 progenies are among the largest known in genetic experiments. The F_2 progenies of wide interracial crosses were normal and healthy. The segregations show that genetic systems underlie the biochemical and physiological processes determining incubation period under the various experimental conditions.

This kind of genetic structure is in contrast with the balanced heterozygotic inversion systems that regulate the ecological races of *Drosophila pseudoobscura*. It also differs from the apparently far less buffered and more highly specialized genetic-physiologic structure of ecological races of *Rana pipiens*, which do not permit even the addition of complete genomes of climatically contrasting races of one species.

The published evidence from the *Lymantria* crossings is extensive but rather inaccessible because of the very size of this classic investigation. In table 68 is presented a highly simplified version of three crossings between climatically extreme races of *Lymantria*. These data, selected from table 1 of one of Goldschmidt's papers (1933*b*), will serve to illustrate the similarity between data from *Lymantria* and data from plants.

The length of the incubation period of six contrasting races is compared in table 68. The eggs were exposed outdoors until February 1, after which they were maintained at a constant temperature of 11° C. The 2-day intervals between classes in Goldschmidt's original table have been combined into 6-day intervals in our shortened version, thereby approaching the 7-day intervals used in grouping dates of flowering in *Potentilla glandulosa*. The class frequencies in reciprocal crosses have been combined into one frequency to simplify tabulation.

At February 1 the embryonic caterpillars inside the eggs had not yet reached the developmental stage "readiness to hatch." Under incubation at 11° C. from February 1 is observed, therefore, an array of hatching dates, reflecting the action of many gene-controlled processes that would have been completed if the incubation had been delayed until the end of April and would have been different if a higher temperature had been maintained.

The three crossings listed in table 68 are between races from different continents. A cross between an early-emerging race from Bukhara in the Turkestan lowland and a late-emerging Mediterranean race from Castel Toblino is listed

TABLE 68

Incubation periods at 11° C. of F_1 and F_2 hybrid progenies between ecological races of Lymantria dispar started February 1, 1933 (after Goldschmidt, 1933*b*)

Races and hybrids	Days of incubation, frequencies of eggs hatched												Totals
	32–37	38–43	44–49	50–55	56–61	62–67	68–73	74–79	80–85	86–91	92–97	98–103	
Bukhara	33	68	10	1	....	....	....	....	...	...	..	..	112
Castel Toblino	..	...	...	....	70	239	51	1	...	...	..	..	361
Castel Toblino × Bukhara													
F_1	..	1	641	1015	228	22	3	....	...	...	..	..	1,910
F_2	..	12	337	2726	6704	2215	640	76	18	5	1	1	12,735
Berlin	..	...	9	186	148	35	16	1	...	...	..	..	395
Matsumoto	..	...	11	21	3	....	....	....	...	...	..	..	35
Matsumoto × Berlin													
F_2	13	231	660	831	411	39	8	....	1	...	..	..	2,194
Massachusetts	..	...	...	29	496	36	5	....	...	...	..	..	566
Portici	..	...	...	....	1	23	145	32	4	...	..	..	205
Portici × Massachusetts													
F_1	..	...	...	....	122	974	644	88	17	1	2	2	1,850
F_2	..	..	...	2	60	845	2758	1316	428	169	30	7	5,615

at the top of the table. The times of emergence of the parental races do not overlap, and both are variable when tested at this stage of development. Because *Lymantria* is an animal organism, there is no way of identifying the particular fraction of the parental genotypes that contributed to the F_1 hybrid. The F_1 was about as variable as the parent races, although definitely intermediate. The F_2 consisted of more than 12,000 individuals, which could have originated from only a small fraction of the F_1 population. In the F_2 the spread in date of emergence extended over more than 2 months and included 25 eggs containing embryos that hatched 2 to 22 days later than the latest caterpillar of the latest parental race. No F_2 eggs hatched as early as the earliest of the early-hatching parental race, and the transgression in lateness is obvious from the table.

The second cross summarized in table 68 is between the continental lowland race from Berlin, Germany, and a montane island race from 581 m. altitude in Japan. The time of hatching of the two parental races is fairly comparable, although the Japanese race probably was slightly the earlier. Data on F_1 progeny are lacking, but the F_2 consisted of nearly 2200 individuals and showed strong transgression in earliness over both parents; 244 F_2 individuals hatched 1 to 2 weeks earlier than the earliest of either parent. Apparently a complementary effect is produced as the genes of these two races are recombined in the F_2. In the former cross the transgression was toward lateness.

In the third cross one parent was of a medium-early race which had been introduced to Massachusetts and succeeded in this environment of cold and fairly long winters. It was crossed with a late-emerging Mediterranean form from Portici, near Naples, Italy. The F_1 showed distinct transgressive segregation toward lateness. In the F_2, consisting of more than 5600 caterpillars, 206 hatched 2 to 16 days later than the late parental race, reinforcing the evidence from the F_1 progeny concerning transgressive segregation.

Data from Goldschmidt's numerous crossings between other racial combinations of *Lymantria dispar* follow patterns similar to those outlined for the three crossings summarized in table 68. The segregations indicate that systems of genes of the multiple kind control processes that lead to hatching. The genes act at various stages in the development of the embryo, and each gene apparently has a minor effect. The direction of the transgressive segregations indicates that some genes tend to lengthen the period of incubation, others to shorten it, and there are also complementary effects. In the absence of genetic analysis of generations beyond the F_2 a full picture of the genetic structure cannot be obtained, but there is sufficient information to indicate the general trend. Most important, the investigations demonstrate that there are mutual interactions among genes, processes, the time element, and the environment. All of them contribute to the control of one observable characteristic, the time of development of an embryo into a caterpillar.

Not all the character differences among races of *Lymantria* are governed by gene systems as complex as the hatching characteristic. The number of molts required for development of larvae to pupae, the presence or absence of certain

larval pigments, and the wing colors are controlled by a series of three allelic genes at one locus, so that monogenic segregation occurs in the hybrids (Goldschmidt, 1933*a*, 1934). Only two of these can be present in any one individual, and most races are homozygous for either one or another of the three. T_1T_1 causes 4 molts of the larvae in both sexes, T_3T_3 causes 5 molts in both, and T_2T_2 4 molts in the male and 5 molts in the female. T_1 produces fast initial growth in the female, and T_3 slows initial growth in the male.

In the control of these and many other racial characteristics of the gypsy moth, Goldschmidt (1934) found that the genetic structure of the species was composed of many elements. Among them he recognized the pattern of multiple genes at one locus, multiple genes at different loci, sex-linked and sex-limited inheritance, and cytoplasmic influence. The genetic and environmental analysis of the hatching period for various ecological races, however, appears to provide the clearest insight into the intricacies of genetic controls that regulate characters of ecological significance.

V

CONCEPTS OF THE GENETIC STRUCTURE OF ECOLOGICAL RACES

In chapters I to III, data bearing on the genetic structure of diverse ecological races of *Potentilla glandulosa* have been presented. In the perspective of researches by many investigators working with diverse kinds of organisms, as outlined in chapter IV, these data lead to certain basic ideas about the genetic structure of naturally occurring evolutionary entities that will be presented in this chapter.

Systems of genes controlling individual characters. Inquiry into the genetic composition of natural entities below the generic level reveals that even the most diverse genera have features reflecting a similar basic genetic structure. The available experimental evidence makes it overwhelmingly clear that paired character contrasts between distinct ecological races, subspecies, and closely related species are regulated by systems of genes of moderate complexity. The genes of these systems are primarily of the polymeric or multiple kind which singly may have relatively minor effects. The components of the gene systems may be of any one of four principal kinds, as follows:

1. *Additive genes,* whose effects are added together, leading to a graded range of expression of a character. Individual genes of an additive series may contribute equally or unequally to the grade of expression. Numerous examples of additive genes have been described in chapters II and IV. Subtractive effects may likewise occur, and such genes are considered to be in this same category although their effects are in the opposite direction.

2. *Epistatic genes,* in which the effect of one covers the expression of others in the series in a definite rank or hierarchy. The most epistatic genes may completely dominate the expression of the succeeding members of the series, but different degrees of epistasis are known to exist. The flower color in *Viola tricolor* reviewed on pages 188 to 190 is a character controlled by such a series.

3. *Oppositional genes,* which have opposite effects and may nullify or inhibit the expression of each other. The resultant balance depends upon the relative strengths of the opposing genes. Examples are seen in the inheritance of palea on the receptacle in *Crepis* (p. 177), and in the control of pappus on the akenes of *Layia* (pp. 191–192).

4. *Complementary genes,* which themselves produce no visible effect, but activate and thus render possible the phenotypic expression of specific other genes of the series. The genes controlling cyanogenesis in legumes as reviewed on pages 199 to 200, and spotted pistils in *Viola* (pp. 187–188), are complementaries. The existence of complementary genes cannot be discovered if both parents are homozygous for one of the two pairs of such a system.

The effect of a system composed of combinations of several of the four classes of genes outlined above is determined by the relative strengths of the component

genes balanced against one another. The phenotypic expression of a character that they regulate depends upon this balance. Since transitions among the four types of genes enumerated above also exist, a great many permutations are possible.

The above categories of genes are of the classic Mendelian kind; they represent loci in different chromosomes, or loci on different parts of the same chromosome sufficiently separated so that their linkage cannot be detected statistically through correlation. The experimental procedures in the present investigations were not precise enough to determine whether any of the individual genes studied are pseudoalleles in the sense of Lewis (1954), whether any represent compound loci as defined by Dunn (1954), or whether they are polygenes according to the concept of Mather (1941, 1943, 1953, 1954). The genes considered here represent major gene entities, but not major chromosomal segments.

Some ambiguity prevails in the usage of "polygene." In one sense, this word has been used to denote a group of genes located very close together on the same chromosome, much like pseudoalleles. It has also been used in a quite different sense, to denote genes influencing the same character but occurring in different chromosomes. In the latter meaning it is interchangeable with "polymeric gene" and "multiple gene" as those terms are used in the present publication.

Although not encountered in the present genetic analysis of *Potentilla glandulosa,* some individual genes of one locus may exist in the form of a series of multiple alleles. In contrast with multiple genes, all the genes of a series of multiple alleles occur at one locus of a chromosome. In a diploid organism, therefore, no more than two members of a multiple allelic series can be present in one individual.

In the diploid *Potentilla glandulosa* the number of genes in multiple nonallelic series governing a single qualitative character was found to range in general between approximately three and six, depending on the character. These estimates are based on various lines of evidence, including the frequency of recovery of parental types in segregating F_2 progeny, and especially the segregation in F_3 populations. The accuracy of the estimates is limited by the size of the population samples and the number of generations available for study. For quantitative characters, the number of contributing genes per character is estimated to be higher and the accuracies are far less.

Ranges of environment within which genes may be expressed. The phenotypic expression of most genes is influenced to some extent by the environment. Above or below certain environmental thresholds the effects of some genes do not appear. Such genes are latent. Activation of the expression of latent genes may induce striking morphological effects when forms possessing them are grown outside their normal range. Examples are seen in the activation of the A_4 gene controlling anthocyanin coloration in *Potentilla glandulosa* at Timberline, as described in chapter II, the modification of flower color of *Primula sinensis* and *Viola tricolor* at different temperatures, and the development of

viviparism in *Deschampsia caespitosa* at a southern latitude, as reviewed in chapter IV.

Not only the activation of a gene but also the degree of expression of an individual gene of a multiple system may depend upon environmental conditions. If an individual plant having genes of opposite effect is cloned and subjected to contrasting environments, spectacular morphological modifications may occur in that individual, as, for example, in the expression of notch in petals of *Potentilla glandulosa,* described in chapter II.

The unanalyzed part of the genotype. Every genetic study is necessarily limited to a comparison of differences. If the two parents of a cross have identical gene complexes for a character, no segregation will appear in the progeny, and the nature of the complexity escapes discovery.

The possibility of penetrating more deeply in the genetic analysis increases if contrasting ecological races are crossed. The parental races of *Potentilla* were highly contrasting in fitness to altitude and to seasonal development, although all came from the same latitude. If, in addition, races from contrasting latitudes had been intercrossed, the detection of hitherto undiscovered groups of genes would have been expected. The presence of such a genetic potential in close relatives of *Potentilla glandulosa* is suggested by extreme modifications in *Potentilla rupestris* L. from central Sweden at 58° N. when transplanted to the Stanford garden at 38° N. (Clausen, Keck, and Hiesey, 1940). Only relatively superficial aspects of the over-all genetic structure of plants have as yet been investigated, and consequently our understanding of gene interaction is imperfect.

It is possible that throughout great sectors of both the plant and animal kingdoms there is a considerable degree of homology in the underlying unanalyzed genetic structure. Evidence of such similarity is found in the homologous variation described by Vavilov (1922) in genetically strongly separated though related species. Additional suggestions of such homology appear in some of the "introgressive" variability described in distinct species (Anderson, 1949). The kinds of gene systems found in ecological races would make it possible for a "new" character to arise without interspecific crossing by means of simple recombinations within the underlying hypostatic gene structure of a single species.

Release of variability. Newly discovered variations are often called "mutations" even though they may have resulted from recombinations that occurred many generations before, within the hypostatic part of the genotype. If an organism is brought into a new environment, the selective pressure upon it will inevitably change in direction. Some of the epistatic genes may thereby become eliminated either through recombination or through true mutation and open the way for previously suppressed portions of the genotype to emerge and come to expression.

Examples of such a release of hidden potential variability are found in the

origin of the annual habit of *Melilotus alba,* which was first noticed when this species was brought to a southern latitude (p. 221), and in strains of milo originally from tropical areas that after many generations became "acclimatized" and succeeded at northern latitudes (p. 229). The recent findings of Scossiroli (1954) of extreme change in progeny of irradiated *Drosophila melanogaster* that became evident only after several generations appear to relate to such a mechanism. Changes in the inner underlying hypostatic gene complex caused by the radiation treatment were apparently not expressed until after a considerable time lag, when they were brought to the surface in subsequent generations. Release of variability can also be brought about simply through the phenotypic expression in new environments of gene effects that were latent, but not evident, in the old.

The crossing of contrasting ecological races greatly increases the likelihood of release of variability transcending that represented by the parental extremes. The interaction among the four basic kinds of gene systems listed in the opening paragraphs of this chapter provides the mechanism for the release. The removal of inhibitors, and the recombination of complementary genes, can produce spectacular changes. In an intergeneric cross between *Layia platyglossa* and *Madia elegans,* for example, the *Madia* parent had no pappus on its akenes, but it nevertheless carried genes that greatly widened the slender bristles in the pappus of *Layia* in the F_1 hybrid. Hybridization, therefore, doubtless plays a role in the continuous dynamic process of adjustment of ecotypes of wild species through environmental selection between genetically variable biotypes.

Coherence of characters distinguishing ecological races. In a diploid species in which the chromosome number is low, as in the 7-chromosome *Potentilla glandulosa,* there is a high statistical probability that at least one of the several genes that control the inheritance of two distinct characters may occur in the same chromosome and close enough together to cause an observable correlation. Such a correlation based on genetic linkage has been demonstrated in *Potentilla glandulosa.* Other genes influencing the same two characters may occur on separate chromosomes, so that the resultant over-all linkage observed is only partial. Consequently, a considerable degree of genetic recombination may still take place among the characters of the parental races. Both morphological and physiological characters may be thus partly linked and share a degree of coherence.

In *Potentilla glandulosa* genetic coherence was also expressed selectively in the index values of the F_2 biotypes surviving at contrasting altitudes (table 47, p. 152). Combined with natural selection, moderate genetic cohesion within the characters of a race tends to ensure its perpetuation as an evolutionary entity. When morphological characters are included in the coherence system, morphologically distinct ecotypic subspecies may result, as in *Potentilla glandulosa.*

Interaction among genes, processes, and environment. The existing balanced interaction among genes, processes, and the ever changing environments

of natural populations is not easily attained, and a reproducible balance cannot be reached in one generation. During the development of a new adjusted balance in organisms as complicated as seed plants a great loss of biotypes occurs, as may be observed in progenies of interspecific crossing.

Natural populations have survived long periods of evolution, and they are so organized that they reproduce a substantial part of the finely balanced, highly intricate genetic structure that is essential for their survival. These entities also have sufficient tolerance to enable them to adjust to fluctuations in the environment over a period of years, and likewise adequate unreleased potential diversity to cope with larger environmental changes during geologic periods. *Potentilla glandulosa* has such a genetic structure, both coherent and flexible. Another example is the *Nicotiana langsdorfii-sanderae* complex, in which Anderson (1939) and Harold Smith (1950) found frequency peaks in F_2 progenies approaching the parental combinations in addition to a considerable degree of recombination.

Little is known about the mechanism by which such flexible gene systems have evolved. Some clues are provided by the intricate genetic-physiologic systems here discussed that characterize ecological races and other subspecific natural entities. The environment is the mold into which the evolutionary entities become adjusted, but the genotypes that are exposed to the molding effect provide the variability for the selection.

Waddington (1942, 1953, 1954) has called attention to the observation that, once a certain line of development has started in an individual, a race, or a species, it tends to become more pronounced with time; it becomes channelized. He suggests that this process is set in motion by competition among various processes for the same biochemical substratum; when a certain direction of activity has started, certain sequences follow.

The idea of channelization is related to the concept advanced by Lerner (1954) under the term "homeostasis." Lerner relates homeostasis to a greater vigor in a heterozygous genetic balance than in a homozygous one. This mechanism seems to be inadequate, however, since many organisms do not necessarily have greater vigor in the heterozygotic condition; heterozygosis by itself is not a sufficient basis to account for the phenomenon of channelization, or of homeostasis.

The details of the interplay between genes and the physiological processes they control are not known. Likewise, there exists a vast unexplored field relating to the manner in which gene-controlled processes influence the morphology of the races and their adjustment to environment. The present data make it overwhelmingly certain, however, that these fields are not separate, but that the causal chain reaches from the gene through biochemical and physiological processes to the morphology of the plant and its adjustment to environment. The recognition that genes of diverse influence exist that may control the same character should aid in charting exploration of this field.

Hybrid vigor. Related to the interaction of different kinds of gene systems is hybrid vigor. The study of hybrid vigor has been promoted largely through the interest in corn genetics, but it is still little understood.

Studies in maize genetics have given rise to the general assumption that major heterosis-producing genes are located fairly close together in the same pairs of chromosomes, and that distinct lineages have different genes for vigor. When genes governing growth that are thus located are brought together in a hybrid, they produce luxuriance in the F_1 and in those F_2 progeny that are equally heterozygous. In recombinations the vigor is lost.

The situation is very different when the genes giving rise to luxuriance are fairly evenly distributed over all the chromosomes, and are not closely linked. Growth-promoting genes of distinct races may then recombine freely, and in certain hybrids it is possible to assemble genes for luxuriant growth that exceed the performance of both parents and of the F_1. Such a situation exists, for example, among progenies resulting from interecotypic crosses in *Potentilla glandulosa* and in the *Achillea millefolium* complex. Hybrid vigor is related to transgressive segregation, and is brought about by recombination of the four major kinds of gene systems mentioned earlier in this chapter.

Hybrid vigor is closely related to environment also, because it is an expression of growth processes. A hybrid that in one environment may be intermediate or even weak as compared with the parents may luxuriate in a contrasting environment. The interaction between the growth-promoting and the growth-retarding processes, both related to environment, is so little understood that prediction of the course along which this field will develop is impossible.

Ecological races as reservoirs of genes. The survival of a species through geological periods depends upon its capacity both to perpetuate itself and to diversify as required by changing environmental conditions. Ecological races and closely related ecological species serve to ensure moderate stability from generation to generation through genetic coherence, and thereby provide separate reservoirs of genes. Each reservoir contains an assortment differing from the others, although some infiltration of genes may take place between the reservoirs.

The storage of genes may assume many forms. Distinct ecological races may have different genes of a simple additive series, or inactive genes that may come to expression under other environmental conditions. Epistasis and suppressor mechanisms may neutralize the effect of other genes in the system, and the genes of two races may complement each other although separately they are inactive. One race may have the key that can unlock the stored potential variability held by another. Opportunities for release of the stored variability are increased during periods of environmental change that force the races to migrate, and thereby augment their chances for crossing.

A species like *Potentilla glandulosa* is endowed with a genetic structure that is singularly versatile and dynamic. During changing geologic periods it can

move with expanding opportunities and occupy environments that are extremely diverse in altitude, in latitude, and in time. In such contrasting environments, distinct biotype compounds become sifted and adjusted, and evolve to new ecological races.

The over-all genetic structure of such a species corresponds fairly closely to a theoretical model which George Harrison Shull (1929*b*) presented 30 years ago at the International Botanical Congress at Ithaca, New York. In discussing the total range of variability exhibited in space and time by a group of freely interbreeding individuals that compose a species, Shull suggested (1) that a central nonvariable and therefore genetically unanalyzable core is common to all individuals of the species; (2) that the genes may differ from individual to individual within the group, and only these differences can be subjected to genetic analysis; (3) that a great potential of genotypic variation exists through recombinations of the genes of category 2; (4) that modifications in phenotypic expression ("inductions") are caused by differences in the environments occupied by the species; and (5) that minor fluctuating changes in phenotypic expression occur through changes in the local environment from day to day and from year to year. The first three categories embody the effects of the hereditary structure of the species, and the last two the effects of environment.

Shull's diagram (1929*b*, fig. 1) outlines in broad terms the major elements that contribute to the genotypic content of a species and to its variation. To a large degree his ideas have been confirmed and expanded through subsequent experimental work, as shown by the numerous examples reviewed in the monumental work by Stebbins (1950).

Our understanding of the composition and function of species has been greatly clarified and amplified since the presentation of Shull's paper. It is now evident that species are composed of genetically distinguishable ecological races and morphological subspecies, each of which is adjusted to its own kind of environment and controlled by interacting systems of genes loosely held together through genetic coherence. It is also clear that through their genetic structure contrasting ecological races offer exceptional sources of hitherto unexpressed variability, and that a causal interaction exists between the gene systems, processes, and the environment.

Shull's first category, the central genotypic core of the species, is still mostly unknown. Even in this area, however, hints regarding the structure of the core are beginning to emerge from studies on interspecific hybridization, as reviewed in chapter IV. These suggest that the genes of the core are not essentially different from those designated in Shull's categories 2 and 3, except that genes from distinct species are not freely interchangeable. Undoubtedly the central core of the species contains an untapped potential for gene-controlled variability that is vastly greater than that of the ecological race.

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INDEX

Abegg, F. A., 195, 271
acclimatization (recombination, mutation, and selection), 266
Achillea, 1, 7, 25–26, 217, 219, 268
  asplenifolia, 217–218
  borealis, 25, 218
    morphological similarity to *A. lanulosa,* 25
    serpentine ecotype of, 245
    sspp. *arenicola, californica, gigantea,* 25
    sspp. *borealis* × *gigantea,* hybrid vigor of, 218–219
  chromosome numbers, 217–218
  collina, 217–218
  ecotypes of, compared with *Potentilla,* 7, 25
  interecotypic hybrids, 218–219
  interspecific hybrids:
    asplenifolia × *setacea,* 218
      × *tomentosa,* 218
  lanulosa, 25, 218
    distribution within *borealis* area, 218
    ssp. *alpicola,* 25
  millefolium, 217
  millefolium complex, 1, 26, 217, 219, 268
    speciation in, compared with *Potentilla glandulosa,* 25
  pannonica, 218
  setacea, 217–218
  stricta, 218
  tomentosa, 217–218
Aconitum columbianum, frost resistance, 104
adaptive value in *Drosophila pseudoobscura,* 249–251
Åkerberg, Erik, 235, 270
albinism in man, 194
alcaptonuria in man, 194
aleurone color in *Zea mays,* 168, 169
alfalfa butterfly, 247
alleles, multiple, *see* genes, multiple allelic
alpine and subalpine species, frost resistance in, 104
amino acids, genetic control of, in *Neurospora,* 194
Anderson, Edgar, 169, 265, 267, 270
Anderson, E. G., 169, 273
Andropogon sorghum, 228; *see also Sorghum vulgare* and *S. halepense*
annuals and biennials in *Melilotus,* 220–222
annuals and perennials:
  in *Lolium,* 224–228
  in *Mimulus,* 214–216
anthocyanin:
  environmental modifications of:
    in forms of *Potentilla glandulosa,* 6, 16, 27, 36
    in *Potentilla glandulosa,* 80–83
    in *Viola arvensis,* 99, 190
    in *Zea mays,* 169–171
  inheritance of:
    in *Crepis capillaris,* 177
    in *Geranium robertianum,* 207
    in *Geum coccineum, rivale,* and *urbanum,* 239–240
    in *Plantago major,* 186–187
    in *Potentilla glandulosa,* 41, 51, 80–88, 109
    in *Viola tricolor* complex, 189–190, 205
    in *Zea mays,* 169, 170–171
  station-to-station shifts in correlation of, 150
apomictic species:
  Calamagrostis purpurea, 235
  of *Poa,* 232–235
    chromosomal variation in, 234–235
apomixis, evolutionary significance of, 232
Arber, Agnes, 228, 229, 270
Armeria maritima:
  ecotypes of, 212–213
  hybrids between subspecies, 213
  structural dimorphism in, 213
Artemisia campestris prostrate at Stanford, 202–203
Ascherson, Paul, 174
Aster occidentalis, frost resistance, 104
atavistic reversion of *Capsella heegeri* to *C. bursa-pastoris,* 174
Atwood, Sanford S., 200, 270
Avena sativa, inheritance in:
    of ligule, 163–164
    of panicle shape, 164–165
    of spikelet color, 163, 164
avens, *see Geum*

Babcock, Ernest B., 176–178, 222, 270
Baker, Herbert G., 207, 212, 270

balance:
  between chromosomal arrangements in *Drosophila pseudoobscura,* 250
  between oppositional genes, 263–264
    in *Cucurbita pepo,* 184
    in *Geum* × *Sieversia,* 242
    in *Layia platyglossa,* 191
    in *Layia* × *Roxira,* 244
    in *Madia elegans,* 206
    in *Mimulus guttatus,* 215–216
    in *Pisum sativum,* 181–183
    in *Potentilla glandulosa* affecting petals:
      coloration, 62–65, 66–67
      notch, 57–61
      orientation, 55
      width, 69–71, 72
    in *Triticum vulgare,* 165, 166
    in *Viola tricolor,* 189–190
Bateson, William, 157, 160–161, 270
Baur, Erwin, 99, 165, 201, 270
Beadle, George W., 168, 169, 194, 270, 273
Bernström, Peter, 219–220, 270
big bluegrass, 233–234
binomial ratios in genetic segregation, 42, 44, 238
biotypes:
  in apomictic *Poa* populations, 234–235
  in *Potentilla glandulosa,* 25
black urine disease, 194
bladder campions, 203, 204
bluegrass, *see Poa*
Böcher, Tyge W., 185, 207, 270
bracts of inflorescence:
  in *Plantago major,* enlarged in variants of, 185–186
  in *Potentilla glandulosa,* 36
    inheritance of number of leaflets in, 40, 49, 93–94, 109
branching, orientation of:
    in *Artemisia campestris,* 201–203
    in *Layia chrysanthemoides,* 205–206
    in *Layia jonesii,* 205
    in *Layia platyglossa,* 190–192, 205
    in *Potentilla glandulosa,* 36, 40, 47, 50, 77–78, 109, 150
bread mold, 194
Brink, R. Alexander, 195, 271
bromegrass, 206
Bromus mollis, ecotypes of, 206
broomcorn, *see Sorghum vulgare*
Bursa, see Capsella
Calamagrostis:
  canadensis, frost susceptibility of, 104
  purpurea, 235
Camelina sativa, 176, 177
  chromosome number, 176
  inheritance of leaf shape and stellate pubescence, 176, 177
Capsella:
  bursa-pastoris, 171–175, 176, 206
    chromosome number, 175
    gene frequency in populations, 175
    inheritance:
      of capsule shape, 174-175
      of leaf shape, 171–174
    latitudinal ecotypes, 206
  heegeri, 173–175, 185
    chromosome number, 175
    disappearance of, 174
    inheritance, *see Capsella bursa-pastoris*
    origin:
      by mutation, 174
      by recombination, 175
  penarthae, inheritance of, 174, 176
  solmsiana, fluctuating variability in capsules of, 175
capsule shape:
  in *Camelina,* similar to *Capsella heegeri,* 175
  in Capsella, inheritance of, 174–175
Casey, Robert S., 32, 271
Castetter, Edward F., 220–221, 271
Cave, Marion S., 177, 270
Chamaebatia, 241
chamaephytes in *Potentilla glandulosa,* 15, 79–80
channelization of evolutionary processes, 267
characters, highly modifiable, 127
    complex genetic control of, 130, 143, 147, 148, 242, 244
Charles, Donald R., 209, 271
Chisholm, A. T., 228-229, 277
chromosome numbers:
  of *Achillea millefolium* complex, 217–218
  of *Armeria maritima,* 213
  of *Bromus mollis,* 206
  of *Camelina sativa,* 176
  of *Capsella* species, 175
  of *Crepis capillaris,* 176
    foetida complex, 177
    vesicaria complex, 178
  of Cucurbita pepo, 184
  of *Deschampsia caespitosa,* 202
  of *Drosophila melanogaster,* 187

chromosome numbers—*continued*
of *Drosophila pseudoobscura,* 248
of *Geranium robertianum,* 207
of *Geum,* polyploidy in, 237, 241
of *Gilia capitata,* 208
of *Hemizonia angustifolia,* 245
of *Holocarpha obconica,* 223
of *Lamium maculatum,* 184
of *Lamium purpureum* complex, 220
of *Layia glandulosa,* 243
of *Layia pentachaeta,* 192
of *Layia platyglossa,* 190
of *Lolium,* 224
of *Lymantria dispar,* 255
of *Madia elegans,* 192
of *Madia sativa,* 224
of *Melilotus alba,* 220
of *Mimulus guttatus* and *M. luteus,* 214
of *Pisum sativum,* 179, 183
of *Plantago lanceolata* and *P. major,* 185
of *Plantago maritima* complex, 211
of *Plantago serpentina,* 211
of *Platanus acerifolia* and *occidentalis,* 246–247
of *Poa ampla* and *P. nevadensis,* 233
of *Poa pratensis* and subspecies, 234
of *Poa scabrella* and *P. secunda,* 233
of *Poa* species, multiples of seven, 233
of *Potentilla glandulosa,* 25, 110
of *Roxira serpentina,* 243
of *Silene cucubalus* and *S. maritima,* 203
of *Sorghum* species, 228–229
of *Trifolium repens,* 199
of *Viola tricolor* complex, 187, 188
chromosomes:
geologic constancy of, in *Platanus,* 247
nature of, 157
class limits of *Potentilla* characters, 38, 40–41, 50–51, 135
at transplant stations:
flowering dates, 139
leaf lengths, 130, 136
rosette widths, 136–137
stem lengths, 137
survival patterns, 140–141
vigor, 138–139
years of survival, 139–140
class values of *Potentilla* characters providing code numbers for analysis, 33, 40, 50, 111, 135
rating of, 38, 47
sum of, equaling index value, 38
Clausen, Jens, 99, 158, 187, 188, 190, 192, 201, 204, 206, 214, 217–218, 223, 232, 235, 236, 243–244, 245, 265, 271–272, 279, 280
cleistogamy in *Mimulus laciniatus* and *M. nasutus,* 214
cline, 27–28
cloning in *Potentilla,* 31, 45
clover, 199–200
coast tarweed, 245–246
coding of data in *Potentilla glandulosa,* 32–35, 131–135
coherence, genetic, *see* genetic coherence
Colias, ecotypes and species of, 247
Collins, Guy N., 195, 272
Collins, Julius L., 177, 272
common denominators in crossing *Rana,* 255
competence in *Lolium,* 225–227, 258
compound loci, 264
Cooper, J. P., 224, 225, 272
Corkill, L., 200, 272
corn, Indian, 167–169; *see also Zea mays*
corolla lobe width in *Gilia capitata,* inheritance of, 208
correlation:
genetic:
as resultant of all genes regulating characters, 111
in *Gilia capitata,* between floral characters, 208
in *Pisum sativum,* seed weight with seed color, internode length, and placenta color, 180
in *Potentilla glandulosa,* 110–122
between station responses of same character, 142, 146
diagrams of degrees of, 115, 121
frequencies of degrees of, 116
groups of correlated characters, 79, 94
of branching habit with stem length, 78
of petal color with length, 113–114
of petal color with orientation, 112–113
of petal notch with orientation, 61
of survival capacity with parental characters, 151–153
of winter activity with leaf length, 33–35
station-to-station shifts in, 150–151
tabulation of, 118–120
in *Solidago sempervirens* complex, 210
negative, 117, 122, 150, 151

correlation, genetic—*continued*
opposite in direction to parents, 116, 122
genetic background of, 110–111, 117, 122
undetected or reduced by counteraction of genes of opposite kind, 122
invalid as indicator of genetic linkage, 110–111, 117, 122
pleiotropic:
in *Pisum,* seed weight with abnormal placenta and violet petals, 181
in *Potentilla,* vigor with length and number of stems and survival, 143, 150–151
correlation coefficient *r,* 35, 61, 113, 114
formulas, 111
levels of significance of, 112
use of punched cards in determining, 111
Cox, Lois M., 235, 272
cranesbill, 207
Crepis:
andryaloides, 178
canariensis, 178
capillaris, inheritance of, 176–177
commutata, 177–178
divaricata, 178–179
eritreënsis, 177–178
foetida complex, inheritance of, 177–178, 263
noronhae, 178
taraxacifolia, 178–179
thompsonii, 177–178
vesicaria complex, inheritance of, 178–179
crossings, diallel:
in *Camelina,* 176
in *Lolium,* 227
cross-pollinating plants, residual variability in, 227, 228
crown height in *Potentilla glandulosa,* 17
inheritance of, 50, 79–80, 109, 150
Cucubalus Behen, 203, 204
Cucurbita pepo, inheritance of fruit shape of, 184
cyanogenesis in legumes:
by complementary enzyme and glucoside genes, 199–200
climatic distribution of genes, 200
cytoplasmic inheritance in *Lymantria dispar,* 262
Czartowski, A., 171, 272

Daday, Hunor, 200, 272
Dahlgren, K. V. Ossian, 175, 239, 272
data:
coding of, 33, 40, 51
methods of obtaining, 31–32
on transplant responses, 31
transfer to punched cards, 33–35
Davey, V. McM., 211, 272, 275
Dawson, C. D. R., 200, 272
deadnettle, 219–220, 221, 222
Demerec, Milislav, 195, 272
Deschampsia:
alpina, viviparous in native habitats, 202
caespitosa, 265
viviparous at low latitude, 202
development channelized with time, 267
diallel crossings, *see* crossings, diallel
diapause, *see* incubation period
Dice, Lee R., 247, 273
dimorphism, structural, in European *Armeria maritima,* 213
diploid organisms having multiple genes:
Crepis, 177–178
Drosophila melanogaster, 187
Lamium maculatum, 184
Layia glandulosa, 244
Layia platyglossa, 191
Madia elegans, 193
Pisum sativum, 179, 182
Plantago major, 186–187
Potentilla glandulosa, 109
diploidization gene in yeast, 196
Dobzhansky, Th., 159, 248–250, 273
dominance:
and temperature in *Drosophila,* 201–202
shifts in, by gene action:
in *Layia,* 190–192
in *Mimulus,* 215, 216
dormancy:
in summer, in *Poa scabrella,* 223
in winter:
in alpine *Achillea borealis,* 218
in alpine *Poa canbyi* and *P. gracillima,* 233
in *Potentilla glandulosa,* 6, 15, 23, 27, 30
inheritance of, 41, 101–103
Drosophila:
melanogaster, 187, 201–202, 247, 266
delayed change in, after irradiation, 266
multiple genes regulating spermothecas, 187
vestigial alleles, expression of, related to temperature, 201–202
persimilis, 159

Drosophila—continued
pseudoobscura, 159, 247–251, 259
altitudinal and seasonal shifts in, 247–249
balanced heterozygote inversion systems of, 250–251, 259
chromosomal arrangements and physiological differences, 249–250
chromosome number, 248
ecotypic adjustment by chromosomal arrangements, 251
inversion heterozygotes, adaptive value of:
shifting with latitude of origin, 250–251
shifting with temperature, 250
inversion segments as supergenes, 249
natural populations, 248
Dryas, 241
Dunn, Leslie C., 264, 273
durra, *see Sorghum vulgare*

ear (inflorescence), inheritance of characters of:
in *Triticum vulgare,* length and density, 165, 166
in *Zea mays,* number of seed rows 167–168
East, Edward M., 167–168, 273
Eckert, W. J., 30, 273
ecological race, *see* ecotypes
ecospecies, 235
of *Geum,* altitudinally and edaphically separate, 236–240
of *Lolium,* differing in life cycle and periodicity, 224–228
of *Platanus,* on separate continents, 246–247
of *Rana,* edaphically separate, 254
ecotypes, 1, 2, 26, 235, 268–269
altitudinal:
in *Achillea lanulosa,* 25, 218
in *Armeria maritima,* 213
in *Geum rivale,* 240
in *Lymantria dispar,* 255
in *Madia elegans,* 222–223
in *Mimulus guttatus complex,* 214–215
in *Plantago maritima,* 212
in *Poa ampla,* 233–234
in *Poa scabrella,* 233
in *Potentilla glandulosa,* 12, 14, 15, 18, 23, 26
in *Rana pipiens,* 252
ecotypes—*continued*
as evolutionary entities, 235
as reservoirs of genes, 268–269
continental, in *Lymantria dispar,* 257
edaphic:
in *Armeria maritima,* 212
in *Mimulus,* of meadows, slopes, ephemeral streambeds, 214–215
in *Plantago maritima,* 211
of serpentine and nonserpentine soils:
in *Achillea borealis,* 245
in *Gilia capitata,* 244
in *Layia glandulosa,* 243–245
in *Salvia columbaria,* 245
genetic coherence in characters of, 155–156, 266
inland and maritime:
in *Achillea borealis,* 7, 25, 218–219
in *Armeria maritima,* 212–213
in *Bromus mollis,* Valley and Coast Range, 206
in *Geranium robertianum,* forest and stony beach, 207
in *Hemizonia paniculata,* 205
in *Layia chrysanthemoides,* 205–206
in *Layia platyglossa,* 190–192
in *Mimulus guttatus* complex, 214–215
in *Plantago maritima,* 211, 212
in *Silene cucubalus-maritima,* 203–204
in *Viola tricolor,* fields, coniferous forests, maritime, 203
latitudinal:
in *Achillea borealis,* 218–219
in *Armeria maritima,* 213
in *Capsella bursa-pastoris,* 206
in *Lymantria dispar,* 255
in *Plantago maritima,* 211
in *Poa pratensis,* 234
in *Potentilla glandulosa,* 12–13
in *Rana pipiens,* 251–252
of apomictic species, differing in chromosome number, 232
physiologically distinct:
in *Achillea,* 217
in *Poa,* 232
seasonal:
in *Hemizonia lutescens,* 222
in *Hemizonia luzulaefolia,* 222
in *Holocarpha obconica,* 223
in *Lamium amplexicaule,* 220
in *Lamium purpureum,* 219, 222
in *Madia elegans,* 192–193, 222–223

ecotypic adjustment of *Drosophila pseudoobscura,* 249
by changes in composition of populations:
with seasons, 248–249
with type of environment, 248–250
by genic-physiologic contents of chromosome segments, 249–250
ecotypic subspecies:
of *Achillea millefolium* complex, 217–219
of *Geum urbanum* complex named as species, 236, 238, 240
of *Gilia capitata:*
along coasts, sspp. *chamissonis, pacifica,* 208
in central Coast Ranges, ssp. *tomentosa,* 208
in interior valleys, sspp. *capitata, staminea,* 208
on dry ranges and foothills, ssp. *abrotanifolia, pedemontana,* 208
within Sierran Transition zone, ssp. *mediomontana,* 208
of *Layia glandulosa,* of contrasting soils, 243–245
of *Madia elegans,* ssp. *densifolia,* 222
of *Mimulus guttatus* complex: *nasutus* and *laciniatus,* 214–217
of *Poa pratensis* named as species, 234
of *Plantago maritima: juncoides* and *maritima,* 211–212
of *Platanus, occidentalis* and *orientalis,* 247
of *Potentilla glandulosa,* 2–5
ssp. *hanseni,* 18–21
ssp. *nevadensis,* 21–23
ssp. *reflexa,* 14–18
ssp. *typica,* 5–14
of *Silene cucubalus,* sspp. *cucubalus* and *maritima,* 203–204
of *Sorghum vulgare* named as species, 228–229
Ehrendorfer, Friedrich, 217–218, 273
Emerson, Rollins A., 167–171, 190, 273–274
endosperm characters in *Zea mays,* inheritance of, 167
environmental influences, 269
affecting selection and differentiation, 24
enzymes:
complementary to glucosides in cyanogenesis, 199–200
in legumes, linamarase, 199–200
in maize pollen, diastase, 195
in relation to petal color of *Lathyrus,* 160
enzymes—*continued*
in yeasts:
β-h-fructosidase, by R_1 to R_3, 198–199
galactozymase, by G, 198
α-glucosidase, by M_1, 197
maltase, by M_2 to M_4, 197–198
evolution:
and genetic mechanisms and environmental expression, 158, 159
and genetic structure of ecotypes, 159, 167, 269
and interacting genetic-physiologic-environmental systems, 159, 266–267
and reproducible balanced natural entities, 267
and the unanalyzed part of the genotype, 265, 269
mathematical theory of, 159
evolutionary entities preserved through genetic coherence, 152–153, 155–156, 266
expression of characters, *see* modification; *also* phenotype

Fernald, Merritt L., 211, 274
Ferris, Roxana, 243
feteria, *see Sorghum vulgare*
Fisher, Ronald A., 111, 112, 159, 274
flax, 199
Flood, M. G., 246, 276
flower color, *see* petal color
flower orientation, inheritance of, in *Silene cucubalus-maritima,* 203–204
flowering:
degree of:
in *Potentilla glandulosa,* 11
in *Silene cucubalus* and *maritima,* 203–204
stages in attainment of, in *Lolium,* 225
flowering date:
in *Potentilla glandulosa,* 11, 27, 36
in *Silene cucubalus* and *maritima,* 203
inheritance of:
in *Geranium robertianum,* 207
in *Gilia capitata,* 208
in *Layia chrysanthemoides,* 205–206
in *Layia platyglossa,* 191, 205
in *Madia elegans,* 192–193
in maritime ecotypes of *Madiinae,* 205
in *Mimulus guttatus,* 214, 216–217
in *Potentilla glandulosa,* 40, 51, 105–108, 109, 139, 144–145, 147–150
in *Sorghum vulgare,* 230–231

flowering date—*continued*
station-to-station shifts of:
in *Potentilla glandulosa,* 106, 108, 139, 144–145, 147–150
in *Sorghum vulgare:*
at different altitudes, 230–231
at long days, 231
fluctuations in phenotypic expression, 269; *see also* modification
in *Geum* × *Sieversia,* 242
in *Layia* × *Roxira,* in development of ray florets, 244
in *Potentilla,* 55, 59, 187
Focke, Wilhelm O., 237, 274
Fraser, A. C., 168, 169, 273
frequency distribution curves in *Potentilla:*
of F_2 segregations:
date of flowering, 107
leaf length, 90, 92
seed weight, 42
stem length, 95, 97
of index values:
Upper Monarch Lake × Santa Barbara, 42
Timberline × Oak Grove, 52
of stem lengths, 19
station-to-station shifts in, 92, 97, 107
frost susceptibility:
in *Potentilla glandulosa:*
inheritance of, 51, 103–105, 109
high negative correlation with vigor at Timberline, 150–151
in subalpine species, 104
fruit fly, *see Drosophila*
fruit rostrum in *Geum,* subgenus *Eugeum,* inheritance of, 240
fruit shape in *Cucurbita,* inheritance of, 184
fruit tail in *Geum,* subgenus *Sieversia,* inheritance of, 242–245

Gajewski, W., 236, 238, 239, 241, 274
Garber, Edward D., 228–229, 274
Gärtner, Carl Friederich von, 236, 274
Gasterosteus aculeatus, fresh- and salt-water ecotypes of, 247
gene-controlled metabolic diseases in man, 194
gene conversion in yeasts, 196
gene pools, 20, 268–269
of ecospecies, 268
in *Geum,* 240
in *Mimulus,* 215
gene pools—*continued*
of ecotypes and ecotypic subspecies, 155–156, 268–269
gene systems, 263–264
evolution of, 267
expression through physiological mechanisms, 91, 106, 108, 147, 149–150
flexibility of, 267
regulating characters:
in *Avena sativa:*
ligule development, 163–164
panicle shape, 164–165
spikelet color, 163, 164
in *Camelina sativa,* leaf shape and pubescence, 176
in *Capsella,* leaf and capsule shapes, 172–175
in *Crepis capillaris,* pubescence, leaf lobing, and anthocyanin, 177
in *Crepis foetida* complex, paleate receptacle and flower color, 177–178
in *Cucurbita pepo,* fruit shape, 184
in fowl, plumage color, 161
in *Geranium,* growth habit and stem color, 207
in *Geum:*
fruit rostrum, 240
fruit tail, 243
gynophore, 239
petal color, 238–239
petal orientation and width, 238
in *Lathyrus odoratus,* flower color, 160–161
in *Layia glandulosa,* akene-enclosing bracts, ray florets, and pappus, 244
in *Layia pentachaeta,* color of ray florets, 192
in *Layia platyglossa,* growth habit, time of flowering, pappus pubescence, 191
in *Lolium,* floral development, 227
in *Madia elegans,* flowering, 193
in *Melilotus alba,* annual and biennial life forms, 221
in *Mimulus guttatus* complex, flowering date, annual life form, 215–217
in *Nicotiana tabacum,* number of stem leaves, 165
in *Pisum sativum:*
seed pod, 181–183
seed weight, 179–181

gene systems, regulating characters—*continued*
in *Plantago major,* inflorescence shape and leaf color, 185–187
in *Potentilla glandulosa:*
anthocyanin, 80–88
flowering date, 106, 107, 108, 148
petal color, 61–65, 66–67
petal length, 71–74, 75
petal notch, 57–61
petal orientation, 54–57
petal width, 65–71, 72
pubescence, 88–89
seed color, 76–77
seed weight, 39–45, 76
sepal length, 74, 76
stem length, 95, 96, 99, 101, 147
winter activity, 102
in *Saccharomyces,* enzyme synthesis, 195–199
in *Sorghum vulgare,* flowering time and plant height, 230–231
in *Tachea nemoralis,* stripes, 171, 172
in *Triticum vulgare:*
grain color, 162–165
length and density of spikes, 165, 166
in *Viola,* pistil spot and petal color, 187–190
in *Zea mays:*
aleurone color, 168, 169
plant color (anthocyanins), 169, 170
seed rows, 167, 168
genera, 235
ecologic adjustments of:
in Gramineae, *Lolium, Poa,* and *Sorghum,* 232
in Madiinae, 224
validity of, in *Geum* and *Sieversia,* 243
genes:
activation of, 264–265
affecting genetic correlation, 151
affecting genetic penetrance, 91, 202
by change in environment:
in *Deschampsia* at lower latitude, 202
in *Lolium rigidum* at 24-hr. day, 226
in *Lymantria dispar* omitting chilling, 256–258
in *Potentilla glandulosa,* 82, 88, 91–92, 108–109
in *Primula* and *Viola* at higher temperatures, 190
in *Sorghum vulgare* at 14-hr. day, 231
genes, activation, by change in environment—*continued*
in vernalized *Lolium perenne* at 9-hr. day, 227
in *Zea mays* in sunlight, 169–170
by complementary genes, 82, 88, 160, 188
possible cause of phenocopies in *Drosophila,* 202
additive, 109, 157, 263
regulating characters:
in *Avena sativa:*
angle of panicle branches, 164–165
black color of spikelets, 163–164
in *Geranium robertianum,* prostrate growth habit, 207
in *Hemizonia angustifolia,* subspecific differences, 245
in *Pisum sativum,* seed weight, pod membrane, and bracteoles, 179–181
in *Plantago major,* red leaf color, 187
in *Potentilla glandulosa:*
seed color, 76–77
seed weight, 42, 43
upcurved petals, 55–56
in *Triticum vulgare:*
grain color, 162, 163
long nodes in ear, 165, 166
in *Viola tricolor:*
growth habits, 204
yellow chromatophores, 189
in *Zea mays,* yellow endosperm color, 167
affecting expression of correlation, 110–111, 117, 122
allelic, *see* genes, multiple allelic
biochemical significance of, 159
complementary, 157, 263
regulating characters:
in *Capsella,* leaf incision, 173–174
in *Crepis capillaris,* leaf lobing and anthocyanin, 177
in fowl, plumage color, 161
in *Lathyrus odoratus,* petal color, 160
in *Layia chrysanthemoides,* upcurved branches, 206
in *Layia platyglossa,* absence of central stem, horizontal branching, 191
in legumes, enzyme and glucoside synthesis, 199–200
in *Lymantria,* incubation period, 161

genes, complementary, regulating characters—*continued*
in *Melilotus alba,* biennial life form, 221
in *Mimulus guttatus,* annual life form, 215–216
in *Pisum:*
bracteoles, 183
pod membrane, 182, 183
in *Potentilla glandulosa,* 59–61, 67–71, 72, 82-85, 87, 109
in *Viola tricolor,* pistil spot, 188
in *Zea mays,* aleurone color, 168, 169
cumulative, *see* genes, additive
developmental:
in *Layia,* bleaching yellow rays, 192
in *Layia* × *Roxira,* inhibiting ray development, 244
in *Lolium,* regulating development and flowering, 224–228
in *Lymantria,* regulating incubation processes, 259–261
in *Pisum,* regulating pod shape, 181–183
in *Potentilla,* bleaching yellow petals, 63
in *Sorghum vulgare,* regulating development and flowering, 230–232
dominant, 157
in *Avena,* multiples: producing ligule, 163–164
in *Camelina,* affecting leaf lobing and stellate pubescence, 176
in *Capsella,* affecting leaf lobing and capsule shape, 173
in *Crepis,* affecting pubescence, paleate receptacle, and ligule color, 177
in *Drosophila,* suppressing development of extra spermothecas, 187
in fowl, producing white plumage, 161
in *Lamium maculatum,* producing zygomorphic flowers, 184
in *Lathyrus odoratus,* 160
in *Madia elegans,* causing early flowering, 193
in *Mattthiola,* 160
in *Pisum,* affecting tip and pod, 182
in *Potentilla glandulosa,* 59, 86, 87, 88
in *Saccharomyces,* activating enzymes, 197, 198
in *Sorghum,* pleiotropic: delaying flowering, lengthening nodes, 230
in *Tachea,* inhibiting stripes, 171, 172
in *Triticum,* shortening spikes, 164, 165

genes, dominant—*continued*
in *Viola,* multiples: basic to anthocyanin production, 188–189
in *Zea mays,* inhibiting aleurone color, 169
early concepts of, 157
enzyme-producing, 159, 160, 197–200
in legumes: Li, linamarase, complementary in cyanogenesis, 199–200
in yeasts:
G, galactozymase, 198
M_1, α-glucosidase, fermenting maltose and sucrose, 197, 199
M_2 to M_4, maltase, 197, 198
R_1 to R_3, β-h-fructosidase, fermenting raffinose and sucrose, 198–199
epistatic, 263
regulating characters:
in *Avena sativa,* spikelet color, 163, 164
in *Crepis,* chrome color in ligules, 177–178
in *Layia chrysanthemoides,* central stem development, 206
in *Layia platyglossa,* early flowering, suppressed floccoseness, upcurved branches, 191
in *Madia elegans,* early flowering, 193
in *Mimulus guttatus,* annual growth habit, 215–216
in *Plantago major,* inflorescence shape, 186
in *Potentilla glandulosa,* 55, 59, 63–64, 65, 71, 72, 88–89, 157
in *Sorghum,* maturity, 230
in *Tachea,* stripes, 171, 172
in *Triticum,* nodes in spike, 164, 165
in *Viola:*
petal color: black to violet, 188–189
petal color: violet to yellow, yellow to ivory, 189–190
pistil spot, 188
in *Zea mays,* aleurone color, 169
expression of, *see* genes, phenotypic expression of
geographic occurrence of:
in *Layia pentachaeta,* regulating flower color, 192
in *Layia platyglossa,* regulating pappus, 192
in *Trifolium repens,* controlling cyanogenesis, 200

genes—*continued*
glucoside-producing, Ac, lotaustralin, in legumes, 199–200
hypostatic:
in *Crepis,* producing lemon yellow ligules, 177–178
in *Madia elegans,* multiples, causing late flowering, 193
in *Potentilla* glandulosa, 55, 59, 63–64, 65, 70, 72, 83
in *Triticum vulgare,* lengthening nodes, 164, 165
inhibiting, *see* genes, subtractive
intensifying (semicomplementary):
in *Sorghum vulgare,* maturity gene, 230
in *Zea mays,* anthocyanin, 169
latent, 83, 202, 228, 264–265
modifying:
in nonpappose *Madia,* widening pappus of *Layia,* 266
in *Viola,* affecting intensity and distribution of anthocyanins, 188–189
multiple allelic, 264
in *Drosophila melanogaster,* vestigial group, 201–202
in *Lymantria,* pleiotropically regulating molting and growth, 261–262
in *Zea mays,* regulating plant color, 169
multiple nonallelic, 39, 157, 263–264
regulating characters:
in *Avena sativa:*
ligule, 163–164
panicle shape, 164–165
spikelet color, 163, 164
in *Camelina,* stellate pubescence, 176
in *Capsella,* capsule shape, 173, 174–175
in *Crepis capillaris,* midrib pubescence, flattened leaf surface, 177
in *Crepis foetida,* paleate receptacle, ligule color, 177, 178
in *Crepis vesicaria,* 178
in *Cucurbita pepo,* fruit shape, 184
in *Drosophila,* spermothecas, 187
in *Geranium,* stems, anthocyanins, 207
in *Geum:*
fruit rostrum, 240
fruit tail, 243
gynophore, 239
petal orientation and width, 238
in *Gilia capitata,* flowering time, width of corolla lobe, 208

genes, multiple nonallelic, regulating characters—*continued*
in *Hemizonia angustifolia,* subspecific differences, 245–246
in *Lamium maculatum,* zygomorphic flowers, 184
in *Layia glandulosa,* length and shape of pappus, 244
in *Layia platyglossa,* branches, flowering, floccoseness, 191
in *Lymantria,* incubation period, 261
in *Madia elegans,* late flowering (hypostatic), 193
in *Melilotus,* life form, 221
in *Mimulus,* annual life form, 215–216
in *Nicotiana,* number of stem leaves, 165
in *Pisum,* 183
convexed pods, 182
seed weight, 179–181
in *Plantago major,* color and variegation of leaves, 186, 187
in *Plantago maritima,* 212
in *Potentilla glandulosa,* 109
anthocyanin color, 80–88
petal color, 62–65, 66–67
petal length, 109
petal notch, 58–61
petal orientation, 55–56
petal width, 69, 70, 71
pubescence, 88–89
seed color, 76–77
seed weight, 44, 76
sepal length, 74, 76
winter activity, 101–102
in *Saccharomyces:*
synthesis of β-h-fructosidase, 198, 199
synthesis of maltase, 197, 198
in *Sorghum,* maturity development, 230–231
in *Tachea,* suppressed shell stripes, 171, 172
in *Triticum:*
grain color, 162–163
lengthened spikes, 165, 166
in *Viola:*
basis for anthocyanin, 188, 189
perennial habit, prostrate stems, 204
in *Zea mays:*
basis for anthocyanin, 169
endosperm color, 167
mutability of, 158

genes—*continued*
oppositional, 44, 263
affecting degree and direction of correlations, 117, 122
in *Avena sativa,* regulating spikelet color, 163, 164
in *Crepis foetida,* regulating paleate receptacle, 177, 178
in *Cucurbita,* affecting fruit shape, 184
in fowl, regulating plumage color, 161
in *Geum,* regulating petal color, 238–239
in *Lathyrus,* regulating flower color, 160
in *Layia chrysanthemoides,* stem, 206
in *Layia glandulosa,* ray florets, 244
in *Layia platyglossa:*
central stem, 191
floccose pappus, 191, 192
flowering, 191
side branches, 191, 192
in *Lymantria,* length of incubation period, 261
in *Madia,* time of flowering, 193
in *Mimulus,* annual and perennial life forms, 215–216
in *Pisum,* growth in pod, 182, 183
in *Plantago major,* shape of inflorescence, 186
in *Potentilla glandulosa:*
petal color, 61–65, 66–67
petal length, 72–73, 74
petal notch, 57–61
petal orientation, 54–57
petal width, 69-71, 72
seed weight, 44, 76
sepal length, 74, 76
in *Triticum,* ear density, 165, 166
in *Viola:*
anthocyanins and yellows of petals, 188–189
pistil spot, 188
in *Zea mays,* aleurone color of seeds, 168, 169
phenotypic expression of, 264–265
degree of, 265
fluctuations in, 55, 59, 187, 242, 244
modifications in:
of *Artemisia* and *Deschampsia,* at lower latitude, 202–203
of *Drosophila* vestigials, by varying hatching temperatures, 201
genes, phenotypic expression of, modifications in—*continued*
of Himalaya rabbit, by varying temperatures of hair development, 201
of *Lolium,* by varying vernalization and daylength, 226–227
of *Lymantria,* by varying chilling, date of incubation, and temperature, 256–258
of *Potentilla glandulosa,* by varying altitude, 57, 59, 63, 73, 80–83, 88, 265
of *Potentilla rupestris,* at lower latitude, 265
of *Sorghum,* by varying day length and altitude, 230–231
of *Zea mays,* by varying illumination and soil fertility, 169–171
pleiotropic:
in Pisum sativum:
affecting several pod characters, 182
affecting petal color, placenta, and seed weight, 181
in *Sorghum,* producing late flowering, more and longer nodes, 230
in *Layia glandulosa* × *Roxira,* producing ray florets and bracts, 243–244
in *Lymantria,* controlling moltings and initial growth, 261–262
polymeric, 44, 157, 161, 167, 264; *see also* genes, multiple nonallelic
processes and environment: interaction between, 157, 159, 160, 193–194, 200–203, 266–267
in *Drosophila pseudoobscura,* 247–251
in *Lolium,* 224–228
in *Lotus* and *Trifolium,* 199–200
in *Lymantria dispar,* 255–262
in *Potentilla glandulosa,* 71, 105–108, 147, 149
in *Rana pipiens,* 251–255
in *Saccharomyces,* 196–199
in *Sorghum,* 228–232
in *Zea mays,* 169–171, 194–195
reservoirs of, *see* gene pools.
single, controlling characters:
in *Geum urbanum* complex, anthocyanin color, 238, 239
in *Lymantria,* moltings and initial growth, 261–262
subtractive, 157, 263
in *Avena,* whitening yellow spikelet color, 163, 164

genes, subtractive—*continued*
in *Crepis:*
inhibiting paleate receptacle, 177
inhibiting midrib pubescence, 177
in *Geranium,* inhibiting red color, 207
in *Geum rivale,* suppressing red color, 239
in *Layia platyglossa:*
reducing pappus floccoseness, 191
suppressing central stem, 206
in *Plantago major,* suppressing branches in inflorescence, 187
in *Potentilla glandulosa,* 109, 157
inhibiting petal notch, 58–61
in *Tachea,* inhibiting stripes, 171, 172
in *Triticum,* shortening spike, 165, 166
in *Viola,* complementaries inhibiting pistil spot, 188
spare, *see* genes, latent; *also* genes, activation of
unexpressed, 83, 202, 228, 264–265
genetic barriers:
in *Achillea,* between diploids and between polyploids, 218
in *Geum,* 241
between *Eugeum* and *Sieversia,* 241–243
within *macrophyllum* and *urbanum* complexes, 241
in *Mimulus,* between *tilingii* and other species, 215
in *Rana:*
between ecotypes of *pipiens,* 253, 254
between *palustris* and *pipiens,* 254, 255
in *Sorghum,* within *Eusorghum* and *Parasorghum,* 229
genetic coherence, 117, 153, 155–156, 266
between characters of parental races and subspecies, 153, 208
between morphological and physiological characters, 266
between taxonomic characters and survival capacity, 152–153
degree of, 117
flexibility in, 155
in *Gilia capitata,* 208
in long-term selection, 152–153
in *Nicotiana langsdorfii-sanderae* complex, 267
in *Potentilla glandulosa,* 117, 153, 155–156
in *Solidago sempervirens* complex, 210
preserving biological entities, 155–156, 266
genetic correlation, *see* correlation, genetic
genetic diversity, unexpressed, 146, 147, 202
genetic drift, 246
in *Potentilla glandulosa,* 28
genetic linkage:
in *Pisum,* controlling seed size and morphology, 180
in *Potentilla glandulosa:*
R and Y_1, 113
regulating petal color, 61
regulating petal size and color, 113–114
in *Saccharomyces,* M_1 and r_1, 199
in *Sorghum:*
Ma_1 and dw_2, 230
Ma_3 and r, 230
genetic-physiologic systems:
in *Cucurbita,* regulating growth of fruits, 184
in legumes, controlling cyanogenesis, 199–200
in *Lolium,* regulating periodicity and life cycle, 224–228
in *Lymantria,* regulating incubation period, 261
in *Madia,* regulating growth rate and flowering time, 192–193
in *Pisum,* regulating growth of pod, 181–183
in *Potentilla glandulosa,* 91
regulating flowering date, 106, 108, 149–150
regulating stem length, 147
in *Saccharomyces,* controlling fermentation, 195–199
in *Sorghum,* regulating growth and flowering time, 228–232
genetic recombination, 269
in *Achillea borealis,* significance for hybrid vigor, 218–219
in *Avena sativa,* 163–165
in *Camelina sativa,* 176
in *Capsella,* 172–175
in *Crepis,* 177–179
in *Geranium robertianum,* 207
in *Geum:*
affecting anthocyanin, 239–240
affecting fruit dispersal, 240–243
affecting fruit rostrum, 240
affecting fruit tail, 242–243
affecting gynophore, 238–239
affecting petal color, shape, and orientation, 238–239

genetic recombination, in *Geum—continued*
affecting taxonomic characters, 239–240, 242–243
in *Holocarpha obconica,* 223
in *Lathyrus odoratus,* 160–161
in *Layia × Roxira,* 244
in *Layia chrysanthemoides,* 205–206
in *Layia pentachaeta,* 192
in *Layia platyglossa,* 190–192, 205
in *Lolium,* 226–227
in *Lymantria dispar,* 259–261
in *Madia elegans,* 192–193
in *Melilotus alba,* 221
in *Mimulus guttatus* complex, 215, 217
in *Nicotiana tabacum,* 165
in *Plantago major,* 185–187
in *Potentilla glandulosa,* 55–56, 58, 60, 62, 66–67, 68, 69, 73, 74, 75, 76, 77, 80, 81, 84–85, 87, 89, 94, 102
at transplant stations:
affecting flowering date, 107, 139, 144–145, 147–150
affecting growth, 123–127
affecting leaf length, 93, 130, 136
affecting rosette width, 136, 137
affecting stem length, 98, 137, 144–145, 146–147
affecting stem number, 138, 144–145
affecting survival pattern, 51, 140–141
affecting vigor, 138–139, 142–146
affecting years of survival, 139–140, 144–145
in *Silene cucubalus-maritima,* 203–204
in *Sorghum vulgare,* 231
in *Tachea nemoralis,* 171, 172
in *Triticum vulgare,* 163–164, 165, 166
in *Viola tricolor* complex, 188–190, 204–205
in *Zea mays,* 167, 168, 169, 170
genetic regulating mechanisms in relation to evolution, 158
genetic structure of natural populations and species, 155–156, 267, 269
coherence, flexibility, and intricacy of, 267
in *Drosophila pseudoobscura,* 248–249, 251
in *Geum urbanum* complex, 239–241
in *Lolium,* 228
in *Lymantria dispar,* 259, 262
in *Nicotiana langsdorfii-sanderae* complex, 267
in *Poa pratensis,* 234–235
in *Rana pipiens,* 254, 259
genetic structure of natural populations and species—*continued*
in *Sorghum vulgare,* 269
theoretical model of, 269
genetics, historical development of, 157–160, 171, 269
genic balance, *see* balance between oppositional genes
genic introgression, 156
of *Geum rivale* characters into *urbanum,* 236, 237
genic migration, *see* genic introgression
genic penetrance, degree of, 264–265
affected by presence of other genes, 61
and activation of genes, 91
and degree of epistasis, 88
and differences in environment, 59, 82, 83, 86, 102
and relative speeds of processes, 81
genotype, unanalyzed part of, 171, 221, 265
genetic core of species, 265
potential source of variability, 265, 269
genotypes and phenotypes:
in *Avena sativa,* 164
in *Capsella,* 173
in *Crepis foetida,* 178
in *Geum coccineum × rivale,* 239
in *Lathyrus odoratus,* 161
in *Layia glandulosa,* 244
in *Layia platyglossa,* 191
in *Madia elegans,* 193
in *Mimulus guttatus* complex, 215, 217
in *Pisum sativum,* 182
in *Plantago major,* 186
in *Potentilla glandulosa,* 55–56, 60, 62, 64, 66–67, 68, 70, 72, 83, 84–85, 87, 89
in *Saccharomyces,* 197–199
in *Sorghum vulgare,* 230, 231
in *Tachea nemoralis,* 172
in *Triticum vulgare,* 166
in *Viola tricolor* complex, 188–189
in *Zea mays,* 169, 170
Gentiana simplex, frost resistance in, 104
Geranium robertianum, ecotypes and inheritance of, 207
Geum, 235–243
aleppicum, 241, 242
bulgaricum (of *Sieversia*), 241
canadense, 242
coccineum, alpine meadow species, 238–241
hispidum, 242
intermedium, natural hybrid, 236

Geum—continued
jankae, natural hybrid, 238
macrophyllum, hybrids of, 241
molle, 241
montanum (of *Sieversia*), hybrids and inheritance of, 241–243
oregonense, 241
pyrenaicum chromosome number of, 241
quellyon, chromosome number of, 241
reptans (of *Sieversia*), hybrids of, 241–242
rivale, 235–243; *see also Geum urbanum* complex
altitudinal ecotypes, 240
chromosome sets in common with *Sieversia,* 242
interspecific hybrids, 241
within complex, 237–240
intersubgeneric hybrids:
with *montanum,* 241–242
with *reptans,* 242
silvaticum, chromosome number of, 241
subgenus *Eugeum,* 241–243
seed dispersal, 240–241
species of, 241, 243
subgenus *Sieversia,* 241–243
alpine nature of, 241
seed dispersal, 241
urbanum complex, 235–241
absence of genetic barriers within, 241
gene pools of species:
marked by distinctness in nature, 237, 240
marked by taxonomic characters, 240
geographic and edaphic occurrences of, 236, 240
hybrids with 13 species of *Eugeum,* 241
hybrids within complex, 236
coccineum × *rivale,* 238–239
natural, 238
rivale × *urbanum,* 237–238
natural 236
rivale pallidum × *rivale,* 239–240
inheritance in:
of anthocyanin, 238–239
of gynophore and length of fruit rostrum, 239–240
of petal color and orientation, 238–239
species within, 240
Gilia capitata, 207–208
ecotypic subspecies *abrotanifolia, capitata, mediomontana, pacifica, pedemontana, staminea,* and *tomentosa,* 208
serpentine ecotype, 244
Gilliland, R. B., 196, 197, 199, 274
glands, *see* pubescence
glucosides, gene-controlled:
linamarin in *Linum* and *Trifolium,* 199
lotaustralin in *Lotus* and *Trifolium,* 199–200
Goldschmidt, Richard B., 158, 194, 201, 202, 255–262, 274–275
Goodwin, Richard H., 209–210, 271, 275
grain color, *see* seed color
Grant, Verne, 208, 275
Gregor, James W., 211–212, 275
growth habit:
in *Artemisia campestris,* changed at low latitude, 202–203
inheritance of:
in altitudinal ecotypes of *Potentilla glandulosa,* 17, 36, 40, 47, 50, 77–78, 79–80, 109, 150
in inland and maritime ecotypes:
of *Geranium robertianum,* 207
of *Hemizonia paniculata,* 205
of *Layia chrysanthemoides,* 205–206
of *Layia platyglossa,* 190–192, 205
of *Viola tricolor,* 203–204
See also life forms, annuals and perennials
Grun, Paul, 214, 235, 271, 272, 275
gynophore, inheritance of, in *Geum rivale* × *urbanum,* 239–240
gypsy moth, *see Lymantria dispar*

Haeckel, E. 228
habitats:
of *Geum rivale* and *urbanum,* 235–236
of *Layia glandulosa* and *"Roxira serpentina,"* 243–245
of *Potentilla glandulosa,* 2–5, 6, 24, 26–28, 36, 47
Haldane, J. B. S., 202, 275
Hall, Harvey M., 10, 222, 270
Hammarlund, Carl, 185–187, 275
Hammond, Dorothy, 184, 280
Hansen, Emil Chr., 196
Harnly, M. L., 202, 275
Harnly, Morris H., 202, 275
Hartung, Marguerite E., 233, 275
Hayes, Herbert K., 165, 168, 273, 276
hayfield tarweeds, 205, 222, 224
Heeger, G., 174
hemicryptophytes in *Potentilla glandulosa,* 21, 22, 79–80

Hemizonia, 205–206, 222–224, 245–246
angustifolia, 245–246
ssp. *macrocephala,* 245
citrina, vernal ecotype of *lutescens,* 222
congesta, 222
congesta complex, 205
vernal and autumnal ecotypes of, 222
lutescens, 205, 222
luzulaefolia, 222
multicaulis, absence of central leader in, 205
paniculata, inland and maritima ecotypes, 205
rudis, autumnal ecotype of *luzulaefolia,* 222
species of, mainly aestival or autumnal, 224
vernalis, vernal ecotype of *Holocarpha obconica,* 223
Henry, A., 246, 276
Heribert-Nilsson, Nils, 158, 276
heterosis (heterozygosis), *see* hybrid vigor
heterozygosity and homeostasis, 267
Heuts, M. J., 247, 276
Hiesey, William M., 190, 214, 217–218, 232, 235, 243–244, 245, 265, 271–272, 276, 279
Himalaya rabbit, 201
Hitchcock, Albert S., 233, 276
Holcus sorghum, see Sorghum vulgare
Hollerith punched cards in analysis of data, 32–35
Holocarpha:
obconica, 223
vernalis, as *Hemizonia,* vernal ecotype of *Holocarpha obconica,* 223
virgata complex, 223
homeostasis, 267
homogentisic acid and alcaptonuria, 194
honey spot (honey guide), 188
Hovanitz, William, 247, 276
Hughes, H. D., 220
Hurst, C. C., 157, 270
Huskins, C. Leonard, 228, 276
hybrid vigor, 268
continued through generations, 99–100, 155, 218–219
in *Achillea borealis,* 218–219
in *Drosophila pseudoobscura,* 249–251
in *Geranium robertianum,* 207
in *Potentilla glandulosa:*
expressed in bulk, 138–139, 142–146, 155
expressed in F_1, 36–37
expressed in F_2, 90, 95–97, 146–147, 155
hybrid vigor, in *Potentilla glandulosa—continued*
expressed in F_3, 99–101
expressed in leaf length, 90
expressed in stem length, 95–97, 146–147
relation to transgressive segregation, 90, 95, 96, 218, 268
shifting with environment, 96–98, 127–130, 144–145, 218–219, 268
shifting with races hybridized, 95–97
through range of environments, 155
hybridization, introgressive, in *Geum urbanum-rivale,* 237
hybrids:
interecotypic:
in *Achillea millefolium complex,* 218–219
in *Armeria maritima,* 212–213
in *Geranium robertianum,* forest × stony beach, 207
in *Hemizonia paniculata,* inland × maritime, 205
in *Holocarpha obconica,* autumnal × vernal, 223
in *Lamium purpureum,* vernal × winter-annual, 219
in *Layia chrysanthemoides,* inland × maritime, 205–206
in *Layia platyglossa,* inland × maritime, 190–192
in *Layia* × *"Roxira,"* 243–245
in *Lymantria dispar,* 259–262
in *Madia elegans,* vernal × autumnal, 192-193
in *Melilotus alba,* annual × biennial, 220–221
in *Mimulus guttatus* complex, 214–217
in *Plantago maritima,* 211–212
in *Potentilla glandulosa:*
alpine × coast range, 29–31
alpine × foothill, 24–25, 29–31
coast range × foothill, 29–31
coast range × mid-altitude meadow, 10
in *Rana pipiens,* 253–254
incompatibility in, 253
in *Silene cucubalus,* inland × maritime, 193–194
in *Viola tricolor,* inland × maritime, 194–195
intergeneric:
Geum rivale × *Sieversia montanum,* 241–243

hybrids, intergeneric—*continued*
Layia platyglossa × *Madia elegans*, 266
interspecific:
Achillea asplenifolia × *setacea*, *asplenifolia* × *tomentosa*, 218
Geum:
coccineum × *rivale*, 238–239
macrophyllum × *oregonense*, 241
macrophyllum × *urbanum* complex, 241
montanum × *rivale*, 241–243
rivale × *urbanum*, 237–238
Lolium perenne × *rigidum*, 225–227
Poa alpina × *pratensis*, 235
Poa ampla × *pratensis*, 235
Poa scabrella × *pratensis*, 235
Rana palustris × *pipiens*, 254
Saccharomyces, 196, 199
Sorghum halepense × *vulgare*, 229
Viola arvensis × *tricolor*, 188
Viola lutea × *tricolor*, 188
intersubspecific:
in *Achillea borealis*, 218–219
in *Armeria maritima*, intercontinental, between mono- and dimorphic forms, 213
in *Crepis foetida* complex, 177–178
in *Crepis vesicaria* complex, 178–179
in *Geum rivale*, *rivale* × *pallidum*, 239
in *Gilia capitata*, 208
in *Hemizonia angustifolia*, 245–246
in *Layia glandulosa*, edaphic, 243–245
in *Mimulus guttatus* complex, 215–217
in *Plantago maritima*, intercontinental, 212
in *Platanus*, intercontinental, 246–247
in *Potentilla glandulosa*:
sspp. *nevadensis* × *reflexa*, 24–25, 29–31
sspp. *hanseni* × *typica*, 10
sspp. *nevadensis* × *typica*, 29–31
sspp. *reflexa* × *typica*, 29–30
in *Silene cucubalus*, sspp. *cucubalus* × *maritima*, 203–204
intervarietal:
in *Geum rivale*, anthocyanous × *pallidum*, 239
in *Sorghum vulgare*:
Dwarf Milo × Early Sooner, 231
Dwarf Yellow × Sooner, 230
spontaneous:
Geum rivale × *urbanum*, 236
in *Melilotus alba*, annuals and biennals, 221

hybrids, spontaneous—*continued*
in *Potentilla glandulosa*, relative scarcity of, 10, 24–25
Platanus acerifolia, *occidentalis* × *orientalis*, 246–247
Sorghum halepense × *vulgare*, 229

Ikeno, S., 187, 276–277
incubation period in *Lymantria dispar*:
inheritance of, 259–261
length and requirement of, in ecotypes, 255–258
index value of characters in *Potentilla*, 34, 38, 52
correlation of, with survival capacity, 152
effect of transgressive segregation on, 49
of F_2 of Timberline × Oak Grove, 49–52
data for, 49
of F_2 of Upper Monarch Lake × Santa Barbara, 38–39, 42
inductions, *see* modification
inflorescence:
in *Potentilla glandulosa*, density of, 36
inheritance of characters of:
in *Avena sativa*, 164–165
in *Plantago major*, 185–187
in *Potentilla glandulosa*, 40, 78–79, 109
in *Triticum vulgare*, 165, 166
in *Zea mays*, 167–168
See also bracts; *and* branching, orientation of
inheritance, quantitative, 157
in *Avena* and *Triticum*, 161–165
in *Crepis vesicaria* complex, 178
in *Hemizonia angustifolia*, 245–246
in *Lymantria dispar*, 261
in *Pisum sativum*, 179–181
in *Potentilla glandulosa*, 44, 76–77, 80–88, 101–102, 127–141
in *Zea mays*, 167–168
inhibitors, *see* genes, subtractive
introgression, genic, 156, 236, 237
inversion heterozygotes of *Drosophila pseudoobscura*, adaptive value of:
from different latitudes, 250–251
from same latitude, 248–250
inversion segments:
as supergenes, 249
inhibiting crossover, 248
Iversen, Johs., 185, 276

Jenkin, T. J., 225, 277
Jenkins, James A., 178, 277

Jinks, J. L., 197, 277
Johannsen, Wilhelm, 158, 277
Johnson grass, *see Sorghum halepense*

kafir corn, *see Sorghum vulgare*
Kameroon grass, 228
kaoliang, *see Sorghum vulgare*
Karper, Robert E., 228–232, 277, 279
Keck, David D., 190, 214, 217, 223, 235, 243–245, 265, 271–272
Kempton, J. H., 195, 272
Kentucky bluegrass, *see Poa pratensis* complex
Kephard, L. W., 220, 279
Kiellander, C. L., 234, 277
Klebs, G., 225, 277
Knowles, Paulden F., 206, 277
Kruckeberg, Arthur B., 245, 277

Lamium:
  amplexicaule, ecotypes, 220
  hybridum, 220
  intermedium, f. *vernale* and f. *aestivale,* 219–220
  maculatum, inheritance of peloric flowers, 184
  purpureum, ecotypes, 219–220, 221, 222
  seasonal dimorphism, 219–220
Lamprecht, Herbert, 181, 183, 277
Lang, Anton, 225, 277
Lang, Arnold, 171, 172, 277
Lang, J. M. S., 211, 272, 275
Lange, Johan, 236, 278
Lathyrus odoratus, 160, 168
Laustsen, O., 196, 282
Lawrence, William E., 202, 218, 278
Lawrence, W. J. C., 194, 278
Layia:
  all species vernal and mesic, 244
  chrysanthemoides, inheritance in ecotypes of, 205–206
  glandulosa, 243–245
    edaphic subspecies, *"Roxira,"* from serpentine, 243
    inheritance in, 244–245
  jonesii, growth habit, 205
  pentachaeta, inheritance in subspecies of, 192
  platyglossa, 190–193, 205, 263, 266
    ecotypes of, 190, 205
    inheritance in:
      of floccose pappus, 191–192, 263
Layia, platyglossa, inheritance in—*continued*
      of flowering date, 190–191, 205
      of growth habit, 191–193, 205
    intergeneric hybrid with *Madia elegans,* 266
    pappus widened by *Madia* genes, 266
    shifts in dominance of characters, 190–192
leaf length in *Potentilla glandulosa,* 11, 20, 23, 36, 47
  and winter activity, 35
  inheritance of, 41, 51, 89–94, 109, 136
  interstation F_2 classification of, 130, 136
  interstation shifts in correlations of, 150
leaf lobing, inheritance of:
    in *Camelina,* 176
    in *Capsella,* 171–174
    in *Crepis capillaris,* 177
leaf number, inheritance of, in *Nicotiana tabacum,* 165
leaf width in *Potentilla,* 11, 20, 23, 36, 47
leaves of *Potentilla,* variation in, 8–9, 11, 20, 23
leaves subtending inflorescence in *Potentilla,* inheritance of leaflet number in, 40, 49, 93–94, 109
Ledum glandulosum, frost resistance in, 104
leopard frog, *see Rana pipiens*
Lerner, I. Michael, 267, 278
Lewis, Edward B., 264, 278
life forms:
  annuals and biennials in *Melilotus,* origin and inheritance of, 220–222
  annuals and perennials:
    in *Lolium,* genetic-physiologic-environmental regulation of, 224–228
    in *Mimulus,* inheritance of, 214–216
  chamaephytes and hemicryptophytes in *Potentilla,* 15, 17, 21, 22, 47
    inheritance of, 79–80
ligule of grass leaf in *Avena,* inheritance of, 163–164
Lilium parvum, frost susceptibility of, 104
Lindegren, Carl C., 159, 196, 198, 278
linkage, genetic, *see* genetic linkage between genes
Liquidambar, geologic age of, 246
locus, loci, compound, 264
Lolium, 224–228, 258, 259
  italicum, annual habit of, 224–225
  perenne, 224–228
    requirements for readiness to flower, 225

Lolium, perenne—*continued*
variability in, 226–227
perenne × *rigidum,* 225
segregation in response to chilling and daylength, 226–227
rigidum, 224–228
annual habit of, 225
residual variability at 24-hour day, 226
Wimmera ryegrass of, 225
species of, adjusted to warm-temperate regions, 232
temulentum, scarcity of residual variability in, 228
Lotus, 199–200
australis, source of lotaustralin, 199
corniculatus, segregating for glucoside reaction, 200
linamarase and lotaustralin in species of, 199, 200
tenuis, occasional individuals carrying glucoside, 200
uliginosus, absence of glucoside in, 200
Löve, Askell, 234, 278
luxuriance, *see* hybrid vigor
Lymantria dispar, 247, 255–262
adaptive characters, 255
developmental stages of, 255–256
diapause, 255–261
ecotypes:
altitudinal and latitudinal, 255
early hatching continental, 257
late hatching Manchurian, 257
slowly developing Mediterranean, 257
various Japanese, 255, 257
emergence of larvae and leafing of food plants, 257, 258
food plants of, 255
genetic structure of, 259, 261, 262
hatching of eggs:
at controlled conditions, 256
outdoors, 257
similarity to periodicity in plants, 258
hybrids:
early × late emerging ecotypes, 259–261
intercontinental, 259–260
lowland × montane ecotypes, 260–261
incubation period:
and chilling, 158
and date of initiation, 256, 257
and genetic characteristics, 256, 258
and temperature, 256–258
and time span for "readiness to hatch," 258

Lymantria dispar—*continued*
interaction between genes, processes, time, and environment, 261
molting regulated by series of alleles, 261–262
sex-limited and -linked inheritance, 262
transgressive segregations, 261
Lymantria monacha, 255

Madia:
elegans, 192–193, 222–223
ecotypes of, 192, 222–223
intergeneric hybrid with *Layia platyglossa,* 266
sspp. *densifolia* × *vernalis,* 192–193
sativa, ecotypes of, 224
Madiinae:
ecologic adjustment of genera of, 224
inland and maritime ecotypes, genic regulation of, 205
nature of species of, 222, 224
McGillivray, J. H., 195, 271
Magnolias, geologic age of, 246
maize:
strains of, 167–169
See also Zea mays
Marsden-Jones, E. M., 203, 204, 278
Martin, John A., 251–254, 278
Mather, Kenneth, 264, 278
Matthiola, inheritance of flower color of, 160
maturity for flowering, 225–228, 230–231, 258
meadow frog, *see Rana pipiens*
Melilotus:
alba, 222
annual × biennial forms, hybrids between, 220–221
× *suaveolens,* 220
var. annua, 220–221
possible origins of, 221, 266
suaveolens, conspecific with *alba,* 220
Mendel, Gregor, 157
milo, *see Sorghum vulgare*
Mimulus:
guttatus complex, 213–217
cleistogamy within, 214
inheritance in:
of annual and perennial growth, 214–216
of date of flowering, 216–217
hybrids: *guttatus* × *laciniatus, guttatus* × *nasutus, guttatus* × *tilingii, laciniatus* × *nasutus,* 215, 217

Mimulus—continued
laciniatus, 214–217
luteus, 214
nasutus, 214–217
tigrinus, 214
tilingii, 214–217
initial genetic isolation of, 215
Mitchell, Herschell K., 202, 281
modification, 269
as characteristic of species, 269
by degrees, 127
developmental:
in *Capsella solmsiana,* capsule shape, 175
in *Layia* × *Roxira,* ray florets, 244
fluctuating, 55, 59, 187, 242, 244, 269
genetic causes of, 91
in *Achillea borealis* at three altitudes, 218–219
in *Artemisia campestris* at low latitude, 202–203
in *Deschampsia caespitosa* at low latitude, 202
in *Drosophila melanogaster* with varying temperature, 201–202
in Himalaya rabbit at varying temperature, 201
in *Lolium* with varying temperature and daylength, 225–226
in *Potentilla glandulosa* at transplant stations:
of anthocyanin, 80–83, 88, 190
of flowering dates, 105–106, 107, 139
of growth, 123–127, 128, 129, 130
of leaf length, 91, 93, 130, 131
of petal color, 63, 201
of petal length, 73
of petal notch, 57, 59
of petal orientation, 55
of rosette width, 136–137
of stem length, 96–98, 137
of stem number, 138
of vigor, 138–139
of years of survival, 139–141
in *Potentilla rupestris* at low latitude, 265
in *Primula sinensis* at high temperatures, 99, 201
in *Sorghum vulgare* at varying daylength and altitude, 230–231
in *Viola* at high temperature, 99, 190, 201
in *Zea*:
with increased light, 169, 170
with low soil fertility, 170
with nutrient deficiency, 170–171
modification—*continued*
with progression of seasons:
in *Holocarpha obconica,* 223
in *Lamium intermedium,* 220
within single flowers, in *Geum* × *Sieversia,* affecting fruit tail, 242
molting in *Lymantria,* inheritance of, 242
monkey flower, *see Mimulus*
monogenic control:
in *Geum urbanum* complex, of anthocyanin, 238, 239
in *Lymantria dispar,* of molting, 261–262
monomorphism in *Armeria maritima,* 213
Moore, John A., 251–254, 278
Morgan, Thomas H., 157
multiple alleles, *see* genes, multiple allelic
multiple nonallelic genes, *see* genes, multiple nonallelic
Müntzing, Arne, 119–120, 235, 278
Murneek, A. E., 225, 279
mutation:
as outcome of hypostatic recombinations, 265
possible origin of *Capsella heegeri,* 174
in *Saccharomyces,* 197
reversed, 198

natural selection, *see* selection, natural
Neurospora, 159
crassa, genetic control of amino acids, 194
Nicotiana:
langsdorfii-sanderae complex, genetic structure, 267
tabacum, quantitative inheritance in, 165
Nilsson, Ernst, 181, 279
Nilsson-Ehle, Herman, 162–165, 174, 279
Nobs, Malcolm A., 217–218, 235, 271, 276, 279
nun moth, 255
Nygren, Axel, 234, 235, 271, 279

oat, *see Avena sativa*
oat strains and types, 161, 164
Onslow, H., 194, 279
Ostenfeld, Carl H., 234, 279
Owen, Ray D., 194, 202, 280

paleate receptacle, inheritance of, in *Crepis foetida* complex, 177, 178, 263
panicle shape, inheritance of, in *Avena,* 164–165
pansies, petal color of, 188

pappus:
in *Layia glandulosa,* inheritance of length and shape of, 244
in *Layia platyglossa,* inheritance of flocoseness of, 191–192, 263
widened by genes from *Madia elegans,* 266
paracorolla in *Silene cucubalus-maritima* complex, inheritance of, 203–204
peas, *see Pisum sativum*
peloric flowers in *Lamium,* 184
penetrance, genic, *see* genic penetrance
perennials, *see* life forms, annuals and perennials
periodicity:
diurnal, in *Achillea,* 217
seasonal:
affecting date of flowering:
in *Achillea borealis* ecotypes, 218
in *Bromus mollis,* 206
in *Geranium robertianum,* 207
in *Layia chrysanthemoides,* inheritance, 205–206
in *Layia platyglossa,* 191, 205
in *Lolium* ecospecies, 224–228
in *Madia elegans,* inheritance, 192–193
in maritime ecotypes of Madiinae, 205
in *Mimulus guttatus* complex, inheritance, 214–217
in *Potentilla glandulosa,* 6, 27
inheritance, 40, 105–108, 144–145, 147–150
in *Silene cucubalus* and *maritima,* 203
in *Sorghum vulgare,* inheritance, 230–231
affecting date of hatching in *Lymantria,* 255–258
genetic-physiological regulation of, 259–261
affecting dormancy period:
in *Achillea borealis,* 218
in *Poa scabrella,* 233
in *Potentilla glandulosa,* 6, 15, 23, 27, 36
inheritance of, 41, 101–103, 109
affecting life cycle:
in annuals and biennials, *Melilotus,* 220–221
in annuals and perennials:
Lolium, 224–228
Mimulus, 214–216
periodicity, seasonal, affecting life cycle—*continued*
in vernals and winter-annuals, *Lamium,* 219–220, 222
within genera of Madiinae, 224
Peromyscus maniculatus, altitudinal and edaphic ecotypes of, 247
Perry, James W., 32, 271
petal color:
inheritance of:
in *Crepis foetida,* 177–178
in *Dahlia* and *Petunia,* genic-biochemical differences of, 194
in *Geum,* 238–239
in *Lathyrus,* 160–161
in *Layia pentachaeta,* 192
in *Matthiola,* 160
in *Potentilla glandulosa,* 40, 50, 61–65, 66–67, 109
shifts in correlations of, 150
in *Viola,* 188–190, 263
modified with temperature, 99
petal length in *Potentilla glandulosa,* 16, 36
inheritance, 40, 50, 71–74, 75, 109
shifts in correlations, 150
petal notch in *Potentilla glandulosa,* 45, 47, 109
inheritance, 50, 57–61
shifts in correlations, 150
petal orientation:
in *Geum,* inheritance, 238
in *Potentilla glandulosa,* 6, 16, 45, 47
inheritance, 50, 54–57, 109
shifts in correlations, 150
petal width:
in *Geum,* inheritance, 238
in *Potentilla glandulosa,* 36, 45, 47
inheritance, 40, 50, 65, 68–71, 72, 109
shifts in correlations, 150
in *Silene cucubalus-maritima,* 203–204
See also corolla lobe width in *Gilia capitata*
phenocopy, 158, 200, 202
in *Deschampsia caespitosa,* 200
in *Drosophila melanogaster,* possible causes of, 202
phenotype, 158
fluctuations in, 55, 59, 187, 242, 244, 269
modifications in, *see* modification
See also genotypes and corresponding phenotypes
phenylalanine, 194
phenylketonuria in man, 194

photoperiod, effect of:
in *Lolium,* on vernalization, 225–227
in *Sorghum vulgare,* activating maturity gene at long days, 231
pickerel frog, 254–255
Pieters, Adrian J., 220, 279
pistil spot in *Viola,* inheritance of, 188
Pisum sativum, 179–183
inheritance in:
of pod shape, 181–183
of seed weight, 179–181
linkage in, of genes controlling seed weight and morphology, 180
pleiotropic effects, 181, 182, 183
strains of:
Falcate, 180
Lolland Raisins, 179
Pois Sabre, 183
Stolz des Marktes, 180
transgressive segregations in, 180
plane, *see Platanus*
plant colors in *Zea mays,* 160, 170–171
Plantago:
alpina, 211
carinata, 211
juncoides, 211, 212
lanceolata, 185, 187
major, inheritance in, 185–187
maritima complex, 210
edaphic, altitudinal and latitudinal ecotypes, 211, 212
geographic subspecies, 212
hybrids between, 211–212
var. *glauca* of, 211, 212
neolithic pollen deposits of, 185
oliganthos, 211
serpentina, chromosome number of, 211
teratological strains of, 185, 187
plantain, *see Plantago*
Platanus:
acerifolia, spontaneous hybrid, 246
geologic age of, 246
occidentalis:
conspecific with *orientalis,* 247
ecologic versatility, 246
× *orientalis,* 246
orientalis, 246–247
racemosa, 247
wrightii (form of *racemosa*), 247
pleiotropic effects:
in *Layia,* on rays florets and bracts, 233–234
pleiotropic effects—*continued*
in *Pisum:*
on four pod characters, 182
on petal color, placenta, and seed weight, 181
plumage color, inheritance of, 161
Poa:
alpina, 235
ampla, altitudinal ecotypes, 233–234
apomictic mechanisms of, 232
in relation to chromosome number, 233, 234, 235
arachnifera, dioeciousness in, 233
arida, 233
canbyi, 233
confinis, dioeciousness in, 233
Dioicopoa, South American section of, 233
douglasii, dioeciousness in, 233
ecological range of, 232
gracillima, 233
juncifolia, 233
macrantha, dioeciousness in, 233
nervosa, dioeciousness in, 233
nevadensis, 233
perennial bunchgrass section of, 233–234
Pratenses section of, 233–234
pratensis complex:
absorption of genomes from diverse species, 235
altitudinal, latitudinal, edaphic ranges of, 234
biotypes of, intermixed in populations, 234–235
hybrids: *alpigena* × *pratensis, ampla* × *pratensis, scabrella* × *pratensis,* 235
recombination between physiologic and taxonomic characters, 235
recovery:
of apomixis, 235
of *pratensis*-like forms, 235
subspecies: *alpigena, angustifolia, arctica, irrigata,* 234
reticulate relations in, 232
rupicola, 233
scabrella, ecotypes, 233
seasonal periodicities in species of, 233
secunda, 233
pod, *see* seed pod
pollination systems:
of European *Armeria maritima,* pollen dimorphism in, 213

pollination systems—*continued*
of *Melilotus,* self-compatibility in, requiring "tripping," 221
of *Mimulus:*
cleistogamy in *laciniatus* and *nasutus,* cross-pollination in *guttatus,* 214
self-compatibility in, 214
See also self-incompatibility
polygenes, 264
polygonic crossings, 176, 227
population complexes spatially isolated:
in *Crepis,* named as species, 179
in *Hemizonia angustifolia,* evolved into subspecies, 245–246
population genetics, 159, 246
populations, local:
evolutionary qualities of, 267
in *Capsella,* introduced, 172, 174, 175
in *Drosophila pseudoobscura,* altitudinal and latitudinal, 247–253
in *Geum rivale* and *urbanum,* adjacent but edaphically separate, 235-236, 240
in *Lamium amplexicaule* and *purpureum,* of seasonal ecotypes, 219–220
in *Lamium intermedium,* of one modifiable ecotype, 220
in *Lotus* and *Trifolium,* and cyanogenesis, 200
in *Lymantria,* of diverse regions, 256–258, 260
in *Madia,* maturing at different seasons, 223
in *Mimulus,* annuals and perennials from diverse climates, 214–217
in *Plantago maritima,* from diverse habitats, altitudes, latitudes, and continents, 211–212
in *Poa,* apomictic, 234–235
in *Potentilla,* from diverse habitats and altitudes, 3, 8–9, 11, 16, 19, 20, 26–28
in *Rana,* from diverse latitudes and altitudes, 251–253
Potentilla glandulosa, 1–156, 177, 179, 190, 192, 203, 208, 214, 236, 237, 238, 240, 243, 248, 259, 264, 265, 266, 267, 268
biological entities of, 2, 25–28
chromosome number, 25
significance in genetic linkage, 110
climatic tolerance of subspecies, 6

Potentilla glandulosa—continued
crossing methods, 29–31
crown habits of subspecies, 6, 17
data on segregations, coded, 131–135
ecotypes of, 12, 14, 15, 18, 23, 26
edaphic subspecies, 5
estimated number of genes governing characters, 109, 264
floral and fruit details, 45
frost tolerance, 104
gene systems, 108–110
hybrids between subspecies:
coding of data on, 32–35, 131–135
nevadensis × *reflexa,* 29–31, 45, 47
nevadensis × *typica,* 29–31, 35–38, 45
reflexa × *typica,* 29–30, 103
Santa Barbara × Oak Grove, winter activity of F_1, 103
spontaneous:
reflexa × *nevadensis,* 24–25
typica × *hanseni,* 10
Timberline × Oak Grove, 45–48
class limits and index values of characters, 50–51
F_2 segregations, 47–48, 50–51
coded, 131–135
F_3 progenies, 49–54
altitudes of seed origins of, 53, 54
list of, 53, 100
genetic correlations, 61, 78, 112–114, 116–117
diagram of, 121
table of, 118–120
genetic linkage, 113–114
index value frequencies in F_2, 49, 52
inheritance of characters:
anthocyanin, 51, 80–86
branching of inflorescence, 50, 77–78
crown height, 50, 79–80
flowering date, 51, 107–108
frost susceptibility, 51, 103–105
leaf length, 51, 91–93
petal color, 50, 62–65, 66–67
petal length, 50, 73–74, 75
petal notch, 50, 62–65, 66–67
petal orientation, 50, 54–57
petal width, 50, 65–71
rosette width, 53, 136–137
stem length, 51, 53, 96–101
winter dormancy, 102–103
parental and F_1 characters, 45, 46, 47
coded, 131

Potentilla glandulosa, hybrids between subspecies, Timberline × Oak Grove —*continued*
transplant station responses of F_2 clones:
in flowering date, 107, 139, 144–145, 147–150
in growth, 123–127
in leaf length, 93, 130, 136
in rosette width, 136–137
in stem length, 98, 137, 144–147
in stem number, 138, 144–145
in survival pattern, 140–141
in vigor, 138–139, 142–146
in years of survival, 139–140, 144–145
Upper Monarch Lake × Santa Barbara, 35–38
class limits and index values of characters, 40–41
example of coded data of, 34
F_2 segregations, 36–38, 40–41
genetic correlations, 33–35, 79, 94, 114–116
diagram of, 115
frequencies of degrees of, 116
index value frequencies in F_2, 38–39
inheritance of characters:
anthocyanin, 41, 86–88
flowering date, 40, 106
frost susceptibility, 105
inflorescence density, 40, 78–79
leaf length, 41, 90
leaflet number, 40, 93–94
petal color, 40, 61–62
petal length, 40, 71–73
petal width, 40, 65, 68–71, 72
pubescence, 41, 88–89
seed color, 41, 76–77
seed weight, 39–45, 76
sepal length, 40, 74, 76
stem length, 41, 95–96
winter dormancy, 41, 101–102
parental and F_1 characters, 36, 37, 45
intergrades between subspecies, 24–25
John Day race of, 12–13
local populations, 2, 3, 11
variations within, 8–9, 11, 16, 19, 20, 22, 26, 27–28
seasonal periodicity in ecotypes of, 6, 15, 23, 27, 36, 103
self-compatibility and -incompatibility within, 6
Potentilla glandulosa—continued
ssp. *ashlandica,* 5
ssp. *ewanii,* 5
ssp. *glabrata,* 5
ssp. *globosa,* 5
ssp. *hanseni,* 3, 4, 6, 9, 11, 16, 18–21, 27, 236
ecotypes, 18
individual variability, 16, 18
leaf variation, 9, 20
life form, 21
ssp. *micropetala,* 5
ssp. *nevadensis,* 3, 4, 6, 9, 11, 16, 17, 19, 21–23, 27, 36, 47
ecotypes, 23
interpopulation variation, 22, 23
intrapopulation variation, 16, 22, 23
leaf variation, 9, 23
life form, 22
seasonal periodicity, 23
ssp. *pseudorupestris,* 5
ssp. *reflexa,* 3, 4, 6, 8, 11, 14–18, 19, 27, 47, 236
ecotypes, 15
individual variability, 15, 16
leaf variation, 8
life form, 15
spontaneous hybrid with ssp. *nevadensis,* 24–25
ssp. *typica,* 3, 4, 5-14, 15, 16, 19, 27, 36
complexity of, 14
dwarf form near ocean, 10
ecotypes within, 12, 14
geographic distribution of, 12
individual variability, 7, 16
interpopulation variation, 7, 16
leaf variation, 8
life form, 15
transitions to *reflexa,* 24
type collection, 12
steps in differentiation of, 26
Potentilla rupestris, modification at low latitude, 265
Price, J. R., 194, 278
Primula sinensis rubra, white at high temperature, 99, 201, 264
processes:
and channelization, 267
and gene action and environmental expression, 71, 105–108, 157, 159, 160, 193–200, 224–232, 255–262, 266–267
Prywer, Czeslawa, 237–239, 279
pseudoalleles, 264

pubescence (including glandular), inheritance of:
in *Camelina sativa,* 176
in *Potentilla glandulosa,* 38, 41, 47, 88–89, 109
punched cards:
for calculation of correlations, 33–35, 111
for description and tabulation of individuals, 34, 131–135
for genetic analysis, 32–35
for listing frequencies of character combinations, 33
for selecting F_2 plants adjusted to specific climates, 153–155
for selecting F_2 plants having specified character combinations, 35
for sorting F_2's into classes of station-to-station responses, 142
Punnett, R. C., 157, 160–161, 270

Quinby, John R., 228–232, 277, 279

r, correlation coefficient, 111, 112
rabbits:
modifications in Himalaya form, 201
skins of dark-colored forms containing tyrosinase, 194
ramet, 31
Rana:
brachycephala, 251
palustris, 254–255
hybrids with *pipiens* normal, 254
pipiens, 247, 251–255, 259
controlled temperature tests of, 251–253
ecotypes:
altitudinal, 252
Costa Rican, 253–254
latitudinal, 251–252
hybrids:
Costa Rica × Vermont normal, 253–254
interecotypic abnormal, 253
interspecific, 254
intraecotypic normal, 252–253
specialized genetic-physiologic structure of, 254, 259
tolerance ranges of, 251–252
sphenocephala, 251
random fixation in *Potentilla glandulosa,* 28
ratios of segregation in systems of genes:
complementary:
9 : 7, two dominants, 68, 69, 161, 188, 206, 215
ratios of segregation in systems of genes, complementary—*continued*
7 : 9, dominance reversed, 60, 188, 191, 215
27 : 37, three dominants, 168
epistatic:
12 : 3 : 1, two dominants, 164, 186
48 : 12 : 3 : 1, three dominants, 172
48 : 15 : 1, one epistatic and two hypostatic multiples, 193
9 : 3 : 4, epistatic, and hypostatic intensifier, 230
independent, 9 : 3 : 3 : 1, two dominants, 173
multiple:
3 : 1, one dominant, 60, 62, 69, 78, 85, 163, 164, 188, 191, 231, 238, 239
1 : 3, dominance reversed, 60, 69, 188
15 : 1, two dominants, 56, 60, 84, 85, 163, 164, 167, 173, 177, 186, 187, 191
63 : 1, three dominants, 81, 84, 102, 163, 186, 191, 244
255 : 1, four dominants, 184, 186
oppositional:
13 : 3, two dominants, 56, 60, 69, 161, 191, 206, 244
3 : 13, dominance reversed, 191
61 : 3, dominant, and epistatic multiple inhibitors, 55, 215
51 : 13, multiple dominants, and epistatic specific inhibitor, 178, 244
39 : 9 : 3 : 13, independent dominants, and epistatic specific suppressor, 239
various combinations:
57 : 7, multiples, and specific complementary, 215
27 : 9 : 28, independent, and two complementaries, 161
21 : 43, one additive, and epistatic complementary inhibitors, 188
249 : 7, multiples, and specific complementary, 81, 83, 84, 87
220 : 27 : 9, dominant, basic complementaries, and epistatic inhibitor, 169
235 : 21, multiples, specific complementary, and hypostatic oppositional, 69, 72
877 : 147, multiples, complementaries, and hypostatic oppositional, 215
4075 : 21, four multiples, specific complementary, and hypostatic oppositional, 69, 72

Raunkiaer, Chresten, 15, 22, 279
raylessness, inheritance of, 244
rays in Compositae, 177–178, 192, 194, 243–244
readiness to flower:
in *Lolium,* 225–227, 258
in *Sorghum,* 228, 230–231, 258
readiness to hatch in *Lymantria,* 258–259
receptacle, variation of, in *Potentilla,* 36, 45
reduplication, 157
responses, *see* modification
reversion:
"atavistic," of *Capsella heegeri* to *bursa-pastoris,* 174
partial, of *Capsella heegeri* to *solmsiana,* 175
rhizomes in *Potentilla glandulosa,* 36, 47
Roberts, Catherine, 195–199, 282
rosette width in *Potentilla glandulosa:*
in F_2, 136–137
in F_3, 53
Roxira serpentina, inheritance of raylessness in, 244
Ruibal, Rodolfo, 251–253, 279
Russian avens, 241, 242

Saccharomyces, 195–199
cerevisiae, 196, 197–198
genes of, 197
hybrids: × *italicus,* × *validus,* 196
use as top yeast and in baking, 197
"Yeast Foam" strain, 197
chevalieri:
diploidization genes of, 196
other genes of, 198
homothallic reproduction, 196, 199
hybrid, *chevalieri* × *italicus,* 199
chromosomal situation in, 196
cytogenes in, 196
dairensis, 196
diploid and haploid strains, 196
gene conversion in, 196
interspecific hybrids, 196, 199
italicus:
genes of, 199
hybrid, *validus* × *italicus,* 196
linkage in, 199
mangini, 196
multiple, enzyme-promoting genes, 197–199
mutations:
by X-raying, 197–198
Saccharomyces—continued
spontaneous, 198
unisporus, 196
validus, interspecific hybrids of, 196
Saeed, S. W., 225, 272
Salix, interspecific hybrids, 158
Salvia columbaria, serpentine ecotype of, 245
Sandberg bluegrass, 233
Saunders, Edith R., 157, 160–161, 270, 274
Sax, Karl, 246–247, 279
Schiede, 236
Schultz, Walther, 201, 279
Scossiroli, R. E., 266, 279
Scott-Moncrieff, R., 194, 279
sea plantain, 211–212
sea thrift, 212–213
seasonal dimorphism, *see* periodicity, seasonal
seasonal ecotypes, *see* ecotypes, seasonal
seasonal modification, *see* modification, with progression of seasons
seasonal periodicity, *see* periodicity, seasonal
seed color (of dispersal unit):
in *Potentilla glandulosa,* 6, 36, 47
inheritance of:
in *Avena,* 161, 163–164
in *Potentilla,* 41, 76–77, 109
in *Triticum,* 162–165
in *Zea,* 167–169
seed dispersal in *Geum:*
by animals in *Eugeum,* 240–241
by wind in *Sieversia,* 241–242
multiple genic control of, 242–243
seed pod, inheritance of:
in *Capsella,* 174–175
in *Pisum,* 181–185
seed size and weight:
in *Potentilla glandulosa,* 36, 45, 47
inheritance of:
in *Pisum,* 179–181
in *Potentilla,* 39–45, 76, 109
segregation:
genetic, *see* genetic recombination
ratios of, *see* ratios of segregation in systems of genes
transgressive, *see* transgressive segregation
selection:
by sorting machine, among *Potentilla* F_2's, 153–156
evolutionary, 267
preserving populations having capacity to vary, 25–28, 153–156, 265–266

selection, evolutionary—*continued*
preserving populations having equilibrium and reproducibility, 267
preserving populations having genetic coherence, 152–153, 155–156, 266
natural, 156, 222
after mutation in epistatic superstructure, 265–266
among ecologic-physiologically distinct variants, 222
following interecotypic crossings, 266
limiting genic infusion between adjacent subspecies, 25, 155–156, 237
selective pressure in new environment, 265
self-compatibility:
in *Armeria,* North American and arctic forms, 213
in *Melilotus,* 221
in *Mimulus,* 214
in *Plantago major,* 185
in *Plantago maritima,* North American forms, 212
in *Potentilla,* 6, 36, 47, 49
in *Sorghum,* 230
self-incompatibility:
in *Armeria,* European forms, 213
in *Layia,* 190
in Madiinae, 245
in *Plantago maritima,* European forms, 212
in *Potentilla,* 6, 36, 47, 49
Senecio triangularis, frost susceptibility of, 104
sepal length in *Potentilla glandulosa,* 36
inheritance, 40, 74, 76, 109
sepal orientation in *Geum,* inheritance, 238
serpentine soils, selective effect on plants, 244–245
shepherd's purse, *see Capsella bursa-pastoris*
Shull, George H., 171–175, 206, 269, 280
Sieversia congeneric with *Geum,* 243
Silene cucubalus-maritima complex:
ecotypes, 203
F_2 segregation, 204
Sinnott, Edmund W., 184, 280
Sirks, M. J., 184, 280
Smith, Harold H., 167, 267, 280
Smith, Hugh B., 220–221, 280
Smith Stanley G., 228, 276
snails, inheritance of stripes on shells, 171, 172
Snedecor, George W., 111, 112, 280
Solms-Laubach, H. Grafen von, 174, 280
Sorghum, 228–231, 258, 259, 266
halepense, 228–229
× *vulgare,* 229
Johnsorgo, spontaneous derivative, 229
nitidum × *vulgare,* 229
Parasorghum subgenus, intraspecific hybrids, 229
purpureo-sericeum × *versicolor,* 229
vulgare, 228–232
activation of Ma_1 gene with long days, 231
culture area in United States, 229–230
ecological adaptation of, 231–232
heredity of, 230–232
history of cultivation of, 229
hybrids:
Dwarf Milo × Early Sooner, 231
Dwarf Yellow × Sooner, 230
hypostatic intensifier genes, 230
vulgare complex, genetically intercompatible, wild species of: *arundinaceum, caudatum, cernuum, drummondii, effusus, guineense, laewisoonii, lanceolatum, margaritiferum, subglabrescens, verticilliflorum, virgatum, vogelianum,* 228
sorgo, *see Sorghum vulgare*
species complexes, 235
Achillea millefolium, 217–219
Armeria maritima, 212–213
Camelina sativa, 176
Capsella bursa-pastoris, 171–175
Crepis foetida, 177–178
Crepis vesicaria, 178–179
Geum macrophyllum, 241
Geum urbanum-rivale-coccineum, 235–241
Gilia capitata, 207–208
Hemizonia congesta, 222
Holocarpha virgata, 223
Lamium purpureum, 219–220
Lolium, 224–228
Mimulus guttatus, 214–216
Plantago maritima, 210–212
Poa ampla, 233–234
Poa pratensis, 234–235
Poa scabrella, 233
Potentilla glandulosa, 1–28
Rana pipiens-palustris, 251–255
Saccharomyces, 195–199
Silene cucubalus-maritima, 203–204

species complexes—*continued*
Solidago sempervirens-rugosa, 209–210
Sorghum vulgare, 228–229
Viola tricolor, 187–190
spermothecas, inheritance in *Drosophila,* 187
spike, *see* inflorescence
spikelet color in *Avena,* 161, 163–164
spikeweed, 224
squash, 184
Srb, Adrian, 194, 202, 280
Statice armeria, 213
Stebbins, G. Ledyard, Jr., 269, 280
stem, inheritance of absence of central:
in *Hemizonia multicaulis,* 205
in *Layia chrysanthemoides,* 205–206
in *Layia platyglossa,* 190–192, 205
stem length, inheritance and variation of:
in *Potentilla:*
in F_1, 36, 47
in F_2, 41, 51, 94–101, 109, 138
in F_3, 53, 99–101
in wild populations, 11, 19, 27
shifts in correlation, 150
station responses, 137, 144–145, 146–147
in *Sorghum,* affected by maturity genes, 231
stem number in *Potentilla,* 138
at stations, 144–145
correlations, 150
stickleback fish, 247
Stipa columbiana, frost resistance in, 104
stream-bank monkey flower, *see Mimulus guttatus*
subgenera:
of *Geum,* 241, 243
of *Sorghum,* 228–229
subspecies, 235
of *Achillea borealis* of contrasting latitudes, 217–219
of *Armeria maritima* of separate continents and latitudes, 213
of *Camelina sativa,* biotic, 176
of *Crepis foetida* complex, geographic, 177–178
of *Crepis vesicaria* complex, geographic, 178–179
of *Geum urbanum* complex, 240
of *Geum coccineum,* altitudinally separate, 238, 240
of *Geum rivale* and *urbanum,* edaphically distinct, 236, 238, 240
subspecies—*continued*
of *Gilia capitata,* 207–208
of *Hemizonia angustifolia,* spatially separate, 245–246
of *Layia glandulosa* of contrasting soils, 243–245
of *Layia pentachaeta,* geographically separate, 192
of *Madia elegans,* seasonally separate, 193
of *Mimulus guttatus,* seasonal and edaphic forms, 214, 216
of *Plantago maritima* of separate continents, 211–212
of *Platanus* of separate continents, 246–247
of *Poa pratensis,* latitudinal, 234
of *Potentilla glandulosa,* altitudinal and edaphic, 2, 5, 14, 18, 21, 26, 36, 45, 47
of *Silene cucubalus,* inland and coastal, 203–204
of *Viola tricolor,* 189, 190
Sudan grass, 228
sugars, fermentation by specific genes of yeast:
galactose by G and slowly by g^s, 198, 199
maltose by M_1 to M_4, 197, 198
melebiose hydrolyzed to glucose and galactose, 198
raffinose by R_1 to R_3, 198
sucrose by R_1 to R_3 and slowly by M_1, 197–198, 199
Sullivan, J. T., 200, 270
suppressors, *see* genes, subtractive
survival in *Potentilla glandulosa* F_2 hybrids at three stations, 139–140, 144–145
correlation with parental characters, 151–153
number of three-station survivors, 155
survival pattern in *Potentilla glandulosa:*
F_2 frequencies, 51
method of classification, 140–141
sweet clover, 221
sweet pea, 160, 168
sycamore, 246
systematic categories, early concepts of, 158

Tabucki grass, 228
Tachea nemoralis, inheritance of stripes on shell, 171, 172
tarweeds, hayfield, 205, 222, 224
Tatum, Edward L., 194

taxonomic characters:
 bound into coherence system, 266
 changed by transplantation, 202
 inheritance of:
  in *Capsella,* 173–176
  in *Crepis,* 176–179
  in *Geum,* 238–240
  in *Layia,* 192
  in *Melanium* violets, 158
  in *Potentilla,* 54–57, 79–80
  in *Salix,* 158
  in *Silene,* 203–204
 of generic significance, in *Geum* × *Sieversia,* 241–243
 of tribal significance, in *Layia* × *Roxira,* 243–245
Tedin, Olov, 176, 280
teratological characters, inheritance of, 185–187
Thalictrum fendleri, frost susceptibility of, 104
Thomas, P. T., 225, 277
tidytip, *see Layia*
tolerance range in *Potentilla glandulosa,* 6, 21
 increased in F_1's and certain F_2's, 123, 125, 127, 129
transgressive segregation, 157
 effect on index values, 49
 genetic causes of, 44, 90, 95, 99
 in *Achillea,* vigor and environment, 218–219
 in *Avena,* panicle types, 165
 in *Capsella,* leaf incision, 173
 in *Crepis vesicaria* complex, 179
 in *Cucurbita,* fruit shape, 184
 in *Geum rivale* × *urbanum,* petal color, 238
 in *Lymantria,* length of incubation period, 261
 in *Mimulus,* flowering date, 216–217
 in *Nicotiana,* number of stem leaves, 165
 in *Pisum,* seed weight, 180
 in *Potentilla:*
  flowering date, 106, 107–108
  frost resistance, 105
  growth responses, 123–127
  leaf length, 90
  petal color, 63, 65
  seed weight, 39
  stem length, 95–97, 99–101
 in *Sorghum,* maturity date, 230
transgressive segregation—*continued*
 in *Triticum,* density of ears, 165, 166
 in *Zea,* number of seed rows, 167–168
 station shifts, 106, 107–108, 218–219
Trifolium repens, 199, 200
 cyanogenesis in, 199–200
Triplett, Edward L., 235, 280
Triticum vulgare:
 inheritance of ear type, 165, 166
 inheritance of grain color, 162–165
tufted hairgrass, 202, 265
Tunis grass, 228
Turesson, Göte, 185, 203, 240, 280
Turrill, W. B., 203, 204, 278 281
tyrosinase specific for skins of dark-colored rabbits, 194

variation, 269
 between ecotypes:
  of *Achillea,* 217
  of *Lymantria dispar,* 256–257
  of *Plantago maritima,* 211
  of *Potentilla glandulosa,* 10–12
  of *Rana pipiens,* 251–254
 between individuals:
  of apomictic *Poa pratensis,* 234–235
  of *Deschampsia caespitosa,* 202
  of *Drosophila pseudoobscura,* 248–250
  of *Plantago maritima,* 211
  of *Potentilla glandulosa,* 7, 8–9, 15, 16, 18, 19, 22, 26
 between local populations:
  of *Lamium,* 219–220
  of *Madia elegans,* 223
  of *Plantago maritima,* 211
  of *Potentilla glandulosa,* 7–10, 11, 16, 19
  of *Trifolium repens,* 200
 between ramets of same clone, *see* modification
 between subspecies:
  of *Achillea borealis,* 218–219
  of *Hemizonia angustifolia,* 245–246
  of *Layia glandulosa,* 243–245
  of *Plantago maritima,* 212
  of *Potentilla glandulosa,* 4, 11, 13, 16, 24–25
 clinal, 27
 continuous, 27–28, 161, 167; *see also* inheritance, quantitative
 discontinuous, degrees of, 28, 165
 fluctuating, 269
  in *Geum* × *Sieversia,* 242

variation, fluctuating—*continued*
in *Layia* × *Roxira,* 244
in *Potentilla,* 55, 59, 187
homologous, 265
introgressive, 265; *see also* genic introgression
latent, 264–265
in *Deschampsia,* 202
in *Drosophila,* 202
in *Lolium,* 226–227
in *Lymantria,* 259
in *Potentilla,* 83
in *Sorghum,* 231
revealed by crossing, 68–70, 81–83, 237
random, 27, 28
release of:
by combination of complementary genes, 266
by interecotypic crossings, 123–127, 266
by mutation in epistatic superstructure, 265–266
by planting at different latitude, 202, 229
by removal of inhibitors, 266
by selective pressure in new environment, 221, 265–266
residual, 227–228
untapped potentials of, 269
within species complexes:
of *Achillea millefolium,* 217–218
of *Armeria maritima,* 213
of *Drosophila pseudoobscura,* 247–253
of *Geum urbanum,* 240–241
of *Gilia capitata,* 207–208
of *Hemizonia congesta,* 222
of *Lolium,* 224–225
of *Mimulus guttatus,* 214–216
of *Plantago maritima,* 212
of *Poa pratensis,* 234–235
of *Potentilla glandulosa,* 25–28
of *Solidago sempervirens-rugosa,* 209–210
of *Sorghum vulgare,* 228–229
variegation in *Plantago major,* inheritance, 187
Vavilov, N. I., 265, 281
Veratrum californicum, frost susceptibility in, 104
vernalization:
in *Lolium perenne,* 225–226
in *Lolium rigidum,* 226
Vickery, Robert K., Jr., 214, 217, 281
vigor, degrees of:
a resultant of many processes, 142
hybrid, *see* hybrid vigor
in relation to homeostasis, 267
inheritance of:
in *Achillea,* 218–219
in *Potentilla,* 127–130, 138–139, 141–146
Viola, 158, 187–190, 201, 204–205, 264, 265
alpestris, 189, 190
arvensis, chromosome number, 188
× *tricolor,* 188
kitaibeliana, 189, 190
lutea, 188, 189
Melanium violets, 158
tricolor:
ecotypes, 204–205
old garden form, 189
tricolor complex:
chromosome numbers, 187–188
inheritance:
of growth habit and stem color, 204
of petal color, 188–190, 263
of pistil spot, 188
seasonal shifts in petal color, 99, 190, 201
viviparism, variation in, at low latitude, in *Deschampsia,* 202, 265
Vries, Hugo de, 172, 177, 281

Waddington, C. H., 287, 281
Wagner, Robert P., 202, 281
Walker, Richard B., 244, 281
water avens, 236
waxy endosperm in maize, 195
Weatherwax, Paul, 195, 281
weeds, ecotypes and inheritance:
in *Bromus mollis,* 206
in *Camelina sativa,* 176
in *Capsella bursa-pastoris,* 171–175, 206
in *Lamium* species, 219–220
in *Plantago lanceolata* and *major,* 185–187
Wellensiek, S. L., 181, 281
Wexelsen, Haakon, 187, 281
wheat, 162
strains and types:
Binkelwheat and Poodlewheat, 165, 166
compactum, squarehead, and land wheat, 165, 166
Swedish Velvet, 162
Wheldale, M., 194, 281
Wheldale-Onslow, M., 194, 281

Whyte, R. O., 225, 279
Wiggins, Ira L., 243
Williams, R. D., 200, 281
Wimmera ryegrass, 225
wing area of *Drosophila* vestigials, 201
Winge, Öjvind, 159, 179, 195–199, 236–240, 246, 282
winter activity:
  in *Achillea borealis gigantea,* 218
  in *Poa ampla,* 234
  in *Poa scabrella,* 233
  in *Potentilla glandulosa,* 6, 11, 15, 27
    and leaf length, 35
    inheritance of, 41, 101–103, 109
winter dormancy:
  in *Achillea borealis* ssp. *borealis,* 218
  in forms of *Poa canbyi* and *gracillima,* 233
  in *Potentilla glandulosa,* 6, 11, 12, 14, 15, 23, 27
    F_2's and F_3's of dormant × dormant, 103
Wright, Sewall, 159, 194, 282
Wulff, Thorild, 234

yeast, 159, 195–199

Zea mays, 167–171, 190, 268
  inheritance of characters:
    aleurone color, 168–169
    allelic genes of A_1, B, and R series, 169
    plant colors, 169, 170
    seed rows, 167, 168
    yellow endosperm, 167
  modifications in phenotypic expression, 170, 171
  quantitative inheritance, 168
  waxy endosperm, biochemistry of, 195
zygomorphic (nonpeloric) flowers in *Lamium,* inheritance, 184